CONSERVING PRAIRIE PONDS FOR SWALLOWS: TREE SWALLOW (*TACHYCINETA BICOLOR*) FORAGING AND NESTLING DIET QUALITY IN PRAIRIE AGROECOSYSTEMS

A Thesis Submitted to the
College of Graduate and Postdoctoral Studies
In Partial Fulfillment of the Requirements
For the Degree of Master of Science
In the Department of Biology
University of Saskatchewan
Saskatoon

By

ANDREW STEPHEN ELGIN

PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a Postgraduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professor or professors who supervised my thesis work or, in their absence, by the Head of the Department or the Dean of the College in which my thesis work was done. It is understood that any copying or publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

DISCLAIMER

Reference in this thesis to any specific commercial products, process, or service by trade name, trademark, manufacturer, or otherwise, does not constitute or imply its endorsement, recommendation, or favoring by the University of Saskatchewan. The views and opinions of the author expressed herein do not state or reflect those of the University of Saskatchewan and shall not be used for advertising or product endorsement purposes.

Requests for permission to copy or to make other uses of materials in this thesis in whole or part should be addressed to:

Head of the Department of Biology
112 Science Place
University of Saskatchewan
Saskatoon, Saskatchewan S7N 5E2 Canada

OR

Dean
College of Graduate and Postdoctoral Studies
University of Saskatchewan
116 Thorvaldson Building, 110 Science Place
Saskatoon, Saskatchewan S7N 5C9 Canada

ABSTRACT

Wetland ponds in the Prairie Pothole Region (PPR) of North America are foraging habitat for many avian species; however, the PPR is also agriculturally intensive and expansive, containing most of the cropland in Canada. Tree Swallows (*Tachycineta bicolor*), among other swallows and martins (Family Hirundinidae), forage over ponds and other aquatic habitats to exploit emergent aquatic insects as prey. Swallows may benefit from sources of aquatic insect prey, but they may incur costs, such as pesticide exposure, when foraging in landscapes dominated by cultivated cropland. I investigated the importance of ponds as foraging areas and a factor in insect prey quality for Tree Swallows nesting in prairie agroecosystems. I examined breeding female swallows' foraging habitat selection as well as nestling swallows' omega-3 long-chain polyunsaturated fatty acid (LC-PUFA) status and exposure to neonicotinoid insecticides – two indicators of nestling diet quality potentially influenced by prairie ponds. Based on data from GPS-tagging and a resource selection function (RSF) statistical approach, I found that female swallows more strongly selected for ponds relative to terrestrial habitats. There was a statistically significant increase in relative selection for ponds with distance from the nest, consistent with an energetic trade-off between travelling and use of more profitable foraging patches. I used the ratio of eicosapentaenoic acid (EPA, an omega-3 LC-PUFA) to arachidonic acid (ARA, an omega-6 LC-PUFA) as a qualitative dietary tracer and indicator of omega-3 LC-PUFA intake for swallows. Differences between sites in swallow erythrocyte EPA:ARA ratios were consistent with possible differences in aquatic insect biomass, unrelated to the presence of cropping. Widespread exposure to neonicotinoid insecticides was confirmed via analysis of blood plasma from nestling and adult swallows. Swallows on different study sites differed in exposure, but nestling plasma concentrations of imidacloprid were not strongly associated with amount of cropped area near nests. Nestlings hatched near cultivated cropland had greater plasma concentrations of clothianidin, on average, than those on a grassland-dominated site. Finally, an increase in nestling erythrocyte EPA:ARA ratio was associated with an increase in nestling mass, while no association between plasma total neonicotinoid concentrations and mass was detected. These results have implications for the conservation of aerial insectivores and suggest the importance of conserving and restoring prairie ponds in agroecosystems to ensure the maintenance of biodiversity in the PPR.

ACKNOWLEDGMENTS

I would like to thank my supervisors, Drs. Bob Clark and Christy Morrissey. I sincerely appreciate the opportunity to work with each of you. Thank you for your insights, your constructive criticisms, and your encouragement. Support from each of you has been instrumental. I would also like to thank the other members of my advisory committee, Drs. Tim Jardine and Tracy Marchant. Your comments and suggestions during our meetings are greatly appreciated and have helped to inform my work. Thanks also to my external examiner Dr. Johanna Kraus for her thorough, thoughtful questions and comments.

Thanks to all lab mates for your friendship and support. A special thanks to Dr. Lisha Berzins for training on all things swallows and dedicated assistance in the field and lab. Thanks to the 2017 and 2018 Tree Swallow field crews and all who assisted on Tree Swallow fieldwork. Thanks also to Steve Leach for assistance in placing and repairing swallow nest boxes, to Mark Bidwell for assistance in the delineation of pond margins, to Dr. Chunyan Hao for neonicotinoid analyses of Tree Swallow plasma, and to Dr. Paul Jones for assistance with GC-MS analysis of fatty acids.

I acknowledge several funding sources including the Department of Biology, University of Saskatchewan, the Natural Sciences and Engineering Research Council of Canada (NSERC), Environment and Climate Change Canada, and Nature Saskatchewan.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

6-CNA	6-chloronicotinic acid
ALA	alpha-linolenic acid
ANOVA	analysis of variance
ARA	arachidonic acid
BBS	North American Breeding Bird Survey
BHT	butylated hydroxytoluene
CV	coefficient of variation
DDT	dichlorodiphenyltrichloroethane
df	degrees of freedom
DHA	docosahexaenoic acid
DT_{50}	dissipation time, 50%
EPA	eicosapentaenoic acid
ESA	European Space Agency
FAME	fatty acid methyl ester
GC-MS	gas chromatography – mass spectrometry
GLS	generalized least squares
GPS	global positioning system
HDOP	horizontal dilution of precision
LA	linoleic acid
LC-MS/MS	liquid chromatography tandem mass spectrometry
LC-PUFA	long-chain polyunsaturated fatty acid
LOD	limit of detection
LOQ	limit of quantitation
MCP	minimum convex polygon
MDL	method detection limit
MS	mass spectrometry
NABCI	North American Bird Conservation Initiative
NIST	National Institute of Standards and Technology
NSERC	Natural Sciences and Engineering Research Council of Canada
NWA	National Wildlife Area
PCB	polychlorinated biphenyl
PPR	Prairie Pothole Region
PTFE	polytetrafluoroethylene
PUFA	polyunsaturated fatty acid
RCF	relative centrifugal force
RFID	radio-frequency identification
ROS	regression on order statistics
RSF	resource selection function
SD	standard deviation
SE	standard error
WMO	World Meteorological Organization

CHAPTER 1: GENERAL INTRODUCTION

1.1 Avian Aerial Insectivore Population Trends

Over the past few decades, several species of North American-breeding birds which specialize in feeding on flying insects have experienced population declines in parts of their geographic ranges, according to North American Breeding Bird Survey (BBS) data (Nebel et al. 2010, Sauer et al. 2017). The guild of North American avian aerial insectivores (hereafter, "aerial insectivores") is comprised of flycatchers (Family Tyrannidae), nightjars (Family Caprimulgidae), swallows and martins (Family Hirundinidae, hereafter "hirundines"), and swifts (Family Apodidae). While all members of this foraging guild depredate insects in flight, two general foraging strategies are employed. The hirundines, swifts, and nighthawks (Caprimulgidae: Chordeilinae) are "hawkers," which forage continuously while in flight, while the flycatchers and typical nightjars (Caprimulgidae: Caprimulginae) are "salliers," which capture insects on brief flights away from a perch (e.g., Nebel et al. 2010). Foraging strategy may exhibit some relationship with population trends (hawkers exhibiting synchronicity distinct from salliers), and declines in aerial insectivore populations appear to have been greater among long-distance migrants and populations breeding in northeastern North America (Nebel et al. 2010, Smith et al. 2015, but see Michel et al. 2016). Still, the continent- and guild-wide trend for aerial insectivores may have stabilized more recently according to Breeding Bird Survey data (Sauer et al. 2017), and it is unclear how North American aerial insectivore populations are faring beyond the range of BBS transects. Several hypotheses have been proposed to explain population trends among aerial insectivores, including habitat loss, impacts of environmental contaminants, acid rain, and climatic changes (Spiller and Dettmers 2019). A common reliance on flying insect prey has suggested a hypothesis that declines in certain aerial insectivore populations are related to changes among insect populations or availability of insect prey to aerial insectivores (Nebel et al. 2010, Spiller and Dettmers 2019).

1.2 Intensive Cropping Impacts on Insects and Potential to Impact Aerial Insectivores

Expansion of arable agriculture (crop cultivation) and intensive agricultural practices have been implicated as drivers of avian population declines via impacts on insect prey availability, a phenomenon well-supported in Europe among some terrestrially-feeding birds on farmland (e.g., Benton et al. 2002). There is growing evidence that declines in grassland-breeding birds are, in

part, associated with loss of insect prey attributable to indirect effects of pesticides, but also by intensified grassland agriculture (Brickle et al. 2000, Benton et al. 2002, Boatman et al. 2004, Britschgi et al. 2006, Hart et al. 2006). Hence, it has been suggested that intensive cropping practices might impact aerial insectivorous birds by reducing the abundance of insect prey.

The evidence remains limited that intensive cropping per se affects aerial insectivores via reduction in insect prey. Indirect effects of agricultural pesticides (prey reduction) were even "provisionally ruled out" for Barn Swallows (*Hirundo rustica*) in Europe by Boatman et al. (2004). To my knowledge, the best evidence that intensively cropped landscapes could be associated with lower productivity among any aerial insectivorous species is derived from the study system utilized by Ghilain and Bélisle (2008). Ghilain and Bélisle (2008) assessed several parameters associated with breeding success of Tree Swallows (*Tachycineta bicolor*) along a gradient of intensive cropping and extensive agriculture (i.e., primarily hayfields and pasture). Ghilain and Bélisle (2008) reported that nest box occupancy and clutch size generally decreased with increasing proportions of intensive cultures on the landscape; similarly, the number of fledglings and probability of fledging increased with the proportion of extensive cultures. In the same study system, temporal patterns in abundance (but not biomass) of Diptera and other insects differed in intensively cropped landscapes relative to extensive cultures (Paquette et al. 2013, Bellavance et al. 2018); however, sites characterized by intensive cropping had greater Dipteran abundance in some years (Paquette et al. 2013). Still, Paquette et al. (2014) found no detectable effect of intensive cropping on adult Tree Swallow body mass, though temporal trends (declines in mass) were reported across adult female swallows. Further, Kusack (2018) reported positive association between local intensive cropping and Barn Swallow nestling condition, though this effect was dampened by pre-fledging and no effect on fledging success was reported. Additional work is required to determine whether intensive cropping can influence aerial insectivore performance by reducing insect prey availability.

1.3 Ecological Value of Non-Crop Habitat for Insects and Birds in Agroecosystems

Patches of non-crop habitat in agroecosystems serve as shelter, breeding areas, and foraging habitat for invertebrates and birds, regardless of the overall impact of cropping on insect prey availability (e.g., Mineau and Mclaughlin 1996, Benton et al. 2003). Terrestrial, non-crop habitats in agroecosystems, such as hedgerows and field margins, tend to have greater abundance

and species richness of invertebrates relative to cropped land (Duelli et al. 1999, Thomas and Marshall 1999, Grüebler et al. 2008, Knapp and Řezáč 2015). Some bird species which may breed in agricultural landscapes, including Barn Swallows, appear to select such semi-natural habitats when foraging for insects (Brickle et al. 2000, Evans et al. 2003, Josefsson et al. 2013, Ottens et al. 2014). Consequently, the presence of non-crop habitats may enhance avian diversity in cropland-dominated landscapes (e.g., Heath et al. 2017). This also suggests that for certain farmland-associated birds, the loss of non-crop habitat patches – agricultural expansion – could be an important factor driving population trends (and see Quinn et al. 2017, Stanton et al. 2018). However, it is critical to recognize that avian responses to non-crop habitat are habitat- and species-specific; for instance, grassland-obligate species respond negatively to increases in woody vegetation that can benefit other taxa in agricultural landscapes (e.g., Quinn et al. 2012). Few studies have assessed benefits of aquatic, as opposed to terrestrial, non-crop habitats for insectivorous passerine birds breeding in agricultural landscapes (Davies et al. 2016).

1.4 Importance of Prey Quality to Hirundines: Aquatic Nutritional Subsidies, Contaminant Exposures, and Relationships with Agriculture

Indirect effects (prey reduction) induced by agricultural practices, such as pesticide application, have been demonstrated for terrestrially feeding farmland-associated birds (e.g., Boatman et al. 2004). To my knowledge, only one study has reported possible indirect effects of pesticides on aerial insectivores, though not in relation to agriculture. Poulin et al. (2010) reported that on sites treated with *Bacillus thuringiensis israelensis* (*Bti*) for treatment of mosquitoes, House Martin (*Delichon urbicum*, a hirundine) clutch size and number of fledglings was lower; this was associated with a dietary shift in nestling House Martins. Nestlings on *Bti*-treated sites were fed significantly fewer aquatic Nematoceran Diptera, aquatic dragonflies (Odonata), and arachnid (Araneae) predators, while being fed an increased number of Hymenopterans (terrestrial flying ants). Poulin et al. (2010) reported that the intake of Nematocera, Odonata, and Araneae was positively correlated with breeding success, even on sites without *Bti* treatment. Such findings, among other characterizations of hirundine diets (e.g., Johnson and Lombardo 2000), suggest that hirundines, in particular, exhibit dietary "flexibility" but may incur costs due to reduction in aquatic prey and, presumably, aquatically-sourced nutrients.

Twining et al. (2016) found that supplementing Tree Swallow nestling diets with omega-3 long-chain polyunsaturated fatty acids (LC-PUFA) increased growth rates and mass more than different quantities of food in a factorial experiment. Omega-3 LC-PUFA tend to be substantially more abundant in aquatic insects than in terrestrial insects – a consequence of omega-3 LC-PUFA production by aquatic, but not terrestrial, primary producers (Hixson et al. 2015, Twining et al. 2017). This suggests a hypothesis that aquatic insect availability could be more important than overall insect abundance for breeding Tree Swallow performance. Indeed, Twining et al. (2018) found that the annual fledging success of Tree Swallows was strongly associated with aquatic, but not terrestrial or total, insect biomass.

Prior studies have not convincingly demonstrated that intensive cropping drives a reduction in insects which indirectly impacts aerial insectivores; even studies assessing the importance of insect abundance to swallow reproductive output have reached mixed conclusions (Quinney et al. 1986, McCarty and Winkler 1999a, Imlay et al. 2017, McClenaghan et al. 2019b). Discrepancies between apparent effects of intensive cropping on insects and swallow reproductive output may be attributable to the assumption that total insect abundance is most relevant to swallow performance, rather than abundance of certain insect taxa (e.g., aquatic taxa per Twining et al. 2018) and proximity of productive foraging areas. For example, the "gradient" from extensive agriculture to intensive cropping described by Ghilain and Bélisle (2008) also followed a gradient of agricultural drainage, but Ghilain and Bélisle (2008) did not directly consider aquatic insect availability. Additionally, the presence or absence of productive aquatic habitat (in terms of aquatic insect emergence) is almost certainly more important than spatial variation in water cover for foraging Tree Swallows (e.g., McCarty 1997). Some evidence suggests that effects on swallows in the study system utilized by Ghilain and Bélisle (2008) might be related to reduction in aquatic habitats and aquatic insect prey. Bellavance et al. (2018) reported that abundance of aquatic mayflies (Ephemeroptera) in swallow prey boluses was lower in more intensively cultivated landscapes. Sufficiency of terrestrial insect traps in characterizing "availability" of prey to swallows was also questionable; while mayflies were fairly common in Tree Swallow boluses (~20% individual insects), only two individuals were captured in traps (Bellavance et al. 2018). It is unlikely this represents only intensive prey selection, but rather intensive foraging habitat selection by Tree Swallows; the two mayflies captured in traps were

adults, while all mayflies in boluses were subimagoes (poor-flying immature stages which have not yet emerged or very recently emerged from water).

There is, at present, insufficient evidence for indirect effects of agriculture on aerial insectivores (i.e., prey reductions via pesticide applications); however, there is also potential for direct effects of exposure to agrochemical contaminants among insectivorous birds (e.g., Goldstein et al. 1999). Tree Swallows, especially, are in some sense predisposed to exposure to contaminants in aquatic environments, given the prevalence of emergent aquatic insects in their diets (e.g., Echols et al. 2004, Smits et al. 2005, Maul et al. 2006, Papp et al. 2007, Brasso and Cristol 2008). Still, it should be noted that like other hirundines, Tree Swallows do consume terrestrial insects; aquatic and terrestrial insects may contribute different contaminants (or concentrations thereof) to Tree Swallow diets (McCarty 2001, Smits et al. 2005). Most studies assessing contaminant exposure in swallows have focused on contaminants known to present deleterious effects on birds at relatively low doses, and several of which can be considered legacy contaminants in North America (e.g., dichlorodiphenyltrichloroethane (DDT), polychlorinated biphenyls (PCBs)) (and see McCarty 2001). Additional work is needed to assess exposures of aerial insectivorous species to agricultural pesticides.

1.5 Prairie Ponds: Avian Habitat and Agricultural Impact

The Prairie Pothole Region (PPR) of North America, extending from Iowa, United States to Alberta, Canada, contains several million glacially-formed, depressional wetlands ("prairie potholes") which currently receive most water from precipitation, especially snowmelt (Stewart and Kantrud 1971, Tiner 2003). Throughout this thesis, I refer to "ponds" (primarily Class I through Class V per Stewart and Kantrud 1971) in reference to flooded wetland basins (van der Kamp et al. 2016). The grassland-wetland ecosystem characterizing the PPR provides critical habitat for grassland birds and birds dependent on ponds of variable permanency. To my knowledge, there have been no taxonomically broad assessments of the use of prairie ponds by birds, but use of prairie ponds as foraging habitat by a diversity of avian taxa is unambiguous (and see Shutler et al. 2000). Representatives of at least 17 different avian families make use of ponds as foraging areas during migration or breeding (Elgin, pers. obs.). Likewise, the PPR is perhaps the most productive area for breeding waterfowl in North America (Batt et al. 1989). For the portion of the PPR of the United States, Skagen et al. (2008) estimated that 7.3 million or 3.9

million migratory shorebirds made use of ephemeral ponds during northward or southward migration, respectively. While populations of some North American waterfowl have increased over the past half-century, populations of species reliant on semi-permanent or ephemeral ponds may have experienced declines (NABCI Canada 2012).

Fertile soils and an open landscape have also made the PPR productive for agriculture. The Prairie Provinces of Saskatchewan, Alberta, and Manitoba contain approximately 80% of cropland in Canada (NABCI Canada 2012, Statistics Canada 2016). Consequently, there has been an estimated loss of 70% of native prairie and 40-70% of associated prairie ponds in Canada alone, primarily as a result of agricultural conversion and agricultural drainage, respectively (Government of Canada 1991, Watmough and Schmoll 2007, NABCI Canada 2012). Similarly, historical loss of 60-65% of wetlands basins has been estimated for the portion of the PPR within the United States (Dahl 2014). In the PPR, degradation of vegetated pond margins, drainage of semi-permanent ponds, and conversion to upland has continued; loss and impacts appear most pervasive among semi-permanent or ephemeral ponds (Watmough and Schmoll 2007, Bartzen et al. 2010, Dahl 2014). Commensurate with the extent of agricultural land use, the Prairies account for approximately 80% of the pesticide use in Canada (Kissinger and Rees 2009). Various, primarily agricultural pesticides have been detected in prairie ponds; concentrations of these contaminants sometimes exceed thresholds for protection of aquatic organisms, many of which serve as prey for birds (Mineau and Mclaughlin 1996, Donald et al. 1999, 2001, Main et al. 2014, Goldsborough and Crumpton 2016). Agricultural impacts on the Prairies – including conversion of native grasslands, the drainage, consolidation, and loss of ponds, and widespread pesticide use – have potential to impact bird populations by destroying suitable habitat, reducing prey abundance, and possibly via toxicant exposure (NABCI Canada 2012, Mineau and Whiteside 2013, Gibbons et al. 2015, Sánchez-Bayo et al. 2016).

Prairie ponds may serve as critical foraging habitat for aerial insectivorous birds breeding in agricultural landscapes of the PPR. On sites with prairie ponds, neither overall insect biomass, condition of adult or nestling Tree Swallows, nor apparent survival of adult Tree Swallows appears to be consistently related to the nature of agricultural practice (grazing or cropping), as might be expected if local intensive cropping were a consistent driver of prey reduction for these swallows (unpubl. data., see also Michelson 2015, Stanton 2015). Stanton et al. (2016) reported

that adult Tree Swallow nest visitation – a good proxy for food delivery (McCarty 2002) – was greater on cropland- than grassland-dominated sites with ponds and positively associated with insect biomass; this suggests swallow broods on cropland-dominated sites were fed more often. Michelson et al. (2018) found that the prevalence of aquatic insects in Tree Swallow diets was unaffected by intensive cropping relative to grazing on sites with prairie ponds. Insofar as thresholds of prey intake are met for survival, dietary quality (omega-3 LC-PUFA content and/or aquatic insect consumption) may be more critical than diet quantity for nestling Tree Swallow growth and fledging success (Twining et al. 2016b, 2018). This suggests the presence of productive aquatic habitat – more specifically, greater availability of aquatic insects – could be a stronger driver of Tree Swallow productivity than terrestrial land use practice (e.g., cropping and grazing) in the PPR.

For prairie ponds, impacts of intensive cropping (including pesticide contamination) on insects are probable (e.g., Cavallaro et al. 2019). However, impacts of cropping on insect assemblages appear similar to, if not less severe than, impacts of disturbance by grazing livestock (Anderson and Voncdracek 1999, Tangen et al. 2003, Campbell et al. 2009, Gleason and Rooney 2017). Individual pond characteristics (e.g., pond permanence, presence of fish) have been much more consistently associated with aquatic insect assemblages than agricultural practice (Tangen et al. 2003, Gleason and Rooney 2018). Responses of aquatic insects to disturbance are also complex and taxonomically specific; low-level nutrient inputs and vegetation disturbance by agricultural activity even could increase the emergence of certain tolerant aquatic insect taxa on which Tree Swallows feed (Gabor et al. 1994, Cavallaro et al. 2019).

While swallows can benefit from aquatic insects sourced from ponds as a source of energy and nutrients, they may also be exposed to agricultural pesticides in cropland-dominated landscapes. The neonicotinoid insecticides are one of many widely used pesticides in the PPR and are frequently detected in prairie ponds (Main et al. 2014). Neonicotinoids are a systemic insecticide, typically applied as a seed treatment on crops (Tomizawa and Casida 2005). While the neonicotinoids act selectively on insects – due in part to greater affinity for the target site (nicotinic acetylcholinesterase receptors) in insects (Tomizawa and Casida 2005) – they can exert toxic effects on vertebrates (Gibbons et al. 2015). In birds, exposure to sublethal quantities

of neonicotinoids is most probable. Still, sublethal effects of neonicotinoid intake, especially mass loss due to reduction in feeding, have been reported in several bird species (Lopez-Antia et al. 2013, Eng et al. 2017, 2019, Addy-Orduna et al. 2019). While selective against insects, neonicotinoids and other agricultural pesticides have been detected in Tree Swallow food boluses (Haroune et al. 2015), suggesting that an assessment of swallow exposures to neonicotinoids, among other agricultural pesticides in the PPR, is warranted.

1.6 Tree Swallows as a Study Species

Tree Swallows are hirundine aerial insectivores which breed across much of North America, including in the PPR (Winkler et al. 2011). Tree Swallows will readily breed in nest boxes and are tolerant of human interference, making them easy to capture, mark, and track over time (Jones 2003). These factors make Tree Swallows a good candidate species for examining environmental impacts on hirundines, as well as a "sentinel" species for risks of contaminants and other anthropogenic environmental impacts (McCarty 2001, Jones 2003). BBS data suggest a loss of approximately 45% of the Tree Swallow population in Canada since 1970 (Environment and Climate Change Canada 2017). Interestingly, Tree Swallow populations appear to have increased in the Prairie Provinces of Saskatchewan and especially Alberta over the same period (Environment and Climate Change Canada 2017). The driver(s) of this increasing population trend are unclear and may be partially attributable to increased availability of nest sites, especially in the form of nest boxes (and see Houston and Houston 1998).

The diet of Tree Swallows tends to contain a greater proportion of emergent aquatic insects (i.e., those insects with an aquatic juvenile stage which emerge to a terrestrial adult stage) relative to terrestrial insects – at least when aquatic insects are available (Winkler et al. 2011). Tree Swallows often forage over ponds and other aquatic habitats to exploit emerging aquatic insects as prey (Winkler et al. 2011). Tree Swallows also appear responsive to alterations in aquatic ecosystems and aquatic insect emergence; for example, Tree Swallows increased their "use" of certain individual ponds as foraging areas in response to greater emergent insect densities following nutrient additions and removal of fish (McCarty 1997). Changes in Tree Swallow nestling diet and lowered reproductive success have been associated with alteration and acidification of aquatic ecosystems, most likely related to changes in insect assemblages and/or the quality of prey (e.g., calcium content) (Blancher and McNicol 1988, 1991, St. Louis and

Barlow 1993). Breeding Tree Swallows appear to be, in some regards, reliant upon "healthy" aquatic ecosystems as a source of insect prey, suggesting that aquatic ecosystems act to "subsidize" (Polis et al. 2002) swallow diets with aquatically-sourced energy and nutrients.

1.7 Study Areas

In 2017 and 2018, I monitored Tree Swallows at five established colonies in southcentral Saskatchewan. Two of these colonies, at St. Denis National Wildlife Area (hereafter, "St. Denis") and near the community of Allan Hills (hereafter, "Allan"), were established in areas where tame grass and pasture were the dominant land cover within 8-10 quarter sections (1 quarter section ≈ 0.65 km^2) surrounding nest boxes. Some nest boxes at St. Denis were near cropland (<50 m). Both grassland sites are characterized by grazing (cattle at Allan; cattle and bison at St. Denis), and grazing livestock do reduce terrestrial vegetation structure and can visibly alter or remove vegetated pond margins on both sites (Elgin, pers. obs.). Three sites, near the community of Burr, town of Colonsay, and city of Humboldt (hereafter, referred to by these names) were established in areas where cultivated cropland was the dominant land cover within 8-10 quarter sections surrounding nest boxes (for initial land cover characterization, see Stanton et al. 2016). Crops known to have been present across sites in 2017 and 2018 were canola, peas, and wheat (varieties unknown). Roughly one-quarter of boxes at the Colonsay study site were next to a small area of pasture (1/8 section or ~0.32 km^2). Burr is the most actively drained site, with extensive drainage ditches in cropped fields. Humboldt has experienced recent flooding, with pond water margins expanding over primarily cropped fields. Beginning in 2016 and through 2017, portions of the Humboldt site were also seeded to semi-natural, herbaceous cover which was well-established in 2018.

Given various changes since site establishment, I re-characterized land cover on each study site utilized in the main study year (2018) based on Sentinel-2B satellite imagery (Copernicus Sentinel data 2018, processed by the European Space Agency (ESA); see Chapter 2 for a full description of land cover characterization). Table 1.1 displays a summary of land cover classification on each study site in the main study year (2018) within 1 km of swallow nest boxes. Maps of the study area and each site are provided in Figure 1.1 through Figure 1.6. Imagery was derived from Sentinel-2B true color images (Copernicus Sentinel data 2018, processed by ESA) and maps were created in QGIS (QGIS Development Team 2018). Imagery

was captured just prior to or during crop seeding, such that green areas are non-crop vegetation (including but not limited to grassland, trees, and perennial/herbaceous vegetation).

1.8 Thesis Structure

The overall objective of my thesis was to investigate the importance of prairie ponds to breeding Tree Swallows, especially in relation to agricultural practices in the surrounding terrestrial landscape (cropping or grazing). The specific objectives of my research were to: 1) assess the importance of prairie ponds as foraging habitat for breeding swallows 2) determine whether aquatic insects, sourced from prairie ponds, act as a source of omega-3 LC-PUFA, important to swallow growth and development, and 3) to examine pesticide exposure as a possible trade-off to foraging in cropland-dominated landscapes.

In Chapter 2, I aimed to assess Tree Swallows' use of prairie ponds as foraging areas in agricultural landscapes. I examined habitat use by breeding female Tree Swallows on four study sites (Burr and Colonsay, characterized by cropping; St. Denis, characterized primarily by grassland; and Humboldt, characterized by herbaceous vegetation and cropping). I hypothesized that swallows would select most strongly for ponds, especially relative to cropland, but less strongly relative to grassland or other non-crop terrestrial habitats. I also examined the distribution (abundance and biomass) of insects in different habitat types on these sites in 2017 and 2018, in addition to the grassland-dominated Allan study site utilized in 2017. I hypothesized that spatial variation in insect abundance and biomass would reflect swallow foraging preferences, being greatest near ponds, lower in non-crop vegetation, and lowest in cropped areas.

In Chapter 3, I investigated the potential for aquatic insects, sourced from prairie ponds, to act as a source of omega-3 LC-PUFA for Tree Swallows, and I examined swallows' exposure to neonicotinoid insecticides as a possible trade-off to foraging in agricultural landscapes. I assessed swallows' omega-3 LC-PUFA status on four study sites (Burr and Colonsay, characterized by cropping; St. Denis, characterized primarily by grassland; and Humboldt, characterized by herbaceous vegetation and cropping), and I related differences in swallow omega-3 LC-PUFA status to differences in aquatic insect biomass across sites. I hypothesized that differences among study sites in swallow fatty acid status would reflect differences in the availability of aquatic insects on each site, with greater omega-3 LC-PUFA status associated

with greater aquatic insect biomass. Likewise, I examined swallow exposure to neonicotinoid insecticides, and assessed whether exposure was related to local cropping by comparison across study sites. I hypothesized that sites with cropping in the vicinity of nests would have greater exposure to neonicotinoid compounds than those on a grassland-dominated site. Finally, I assessed whether nestling swallows' omega-3 LC-PUFA status and exposure to neonicotinoid insecticides were associated with positive or negative impacts on nestling mass.

1.9 Authorship

Each data chapter of my thesis is written in manuscript style. Therefore, some redundancy is present in the introduction and methods for each chapter. I am the primary author of each chapter. My co-supervisors, Drs. Bob Clark and Christy Morrissey, procured funding for this research and provided guidance on study design and edits for each chapter. I also collected and analyzed the data, with contributions for neonicotinoid analyses (LC-MS/MS) from Dr. Chunyan Hao and assistance (GC-MS) and guidance on fatty acid analyses from Dr. Paul Jones.

TABLES AND FIGURES

Table 1.1. Summary of land cover (percent cover class) on each study site utilized in 2018. Values represent percentage of 10 m raster cell count within a 1000 m buffer around Tree Swallow nest boxes in June 2018, as based on land cover classification from Sentinel-2B imagery.

Site	Cropland	Non-crop Vegetation	Ponds (Open Water)
Colonsay	81%	8%	10%
Burr	77%	19%	4%
Humboldt	39%	29%	32%
St. Denis	15%	67%	18%

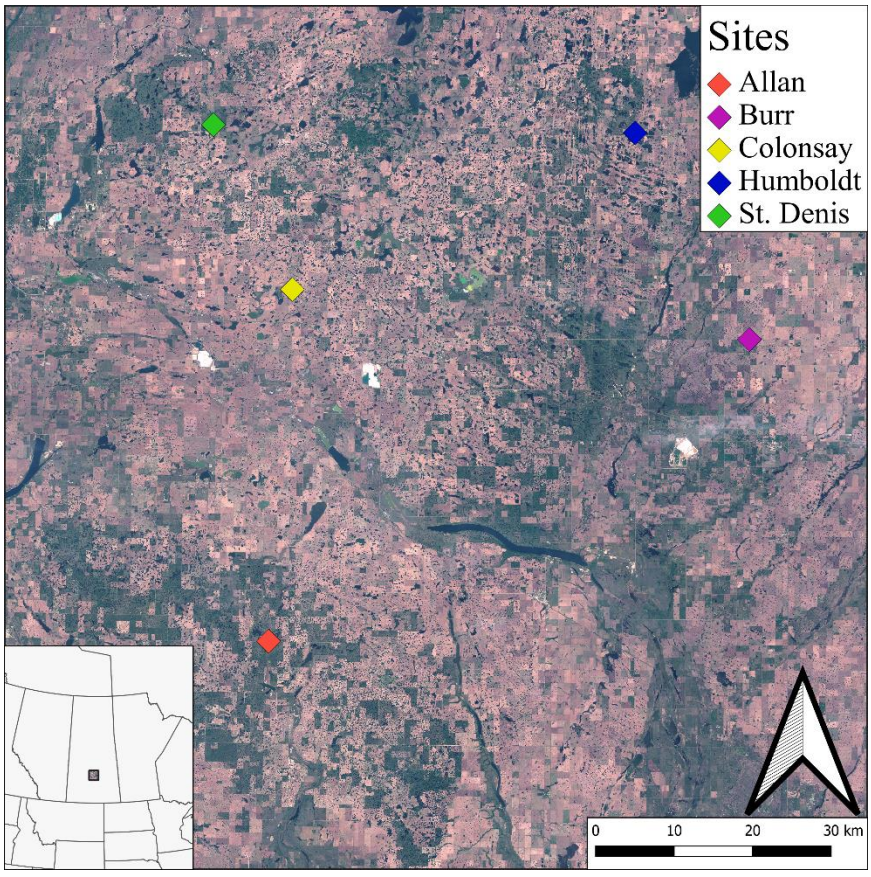

Figure 1.1. Map of the study area in southcentral Saskatchewan. Each study site is represented by colored diamonds. Contains modified Copernicus Sentinel data 2018, processed by ESA.

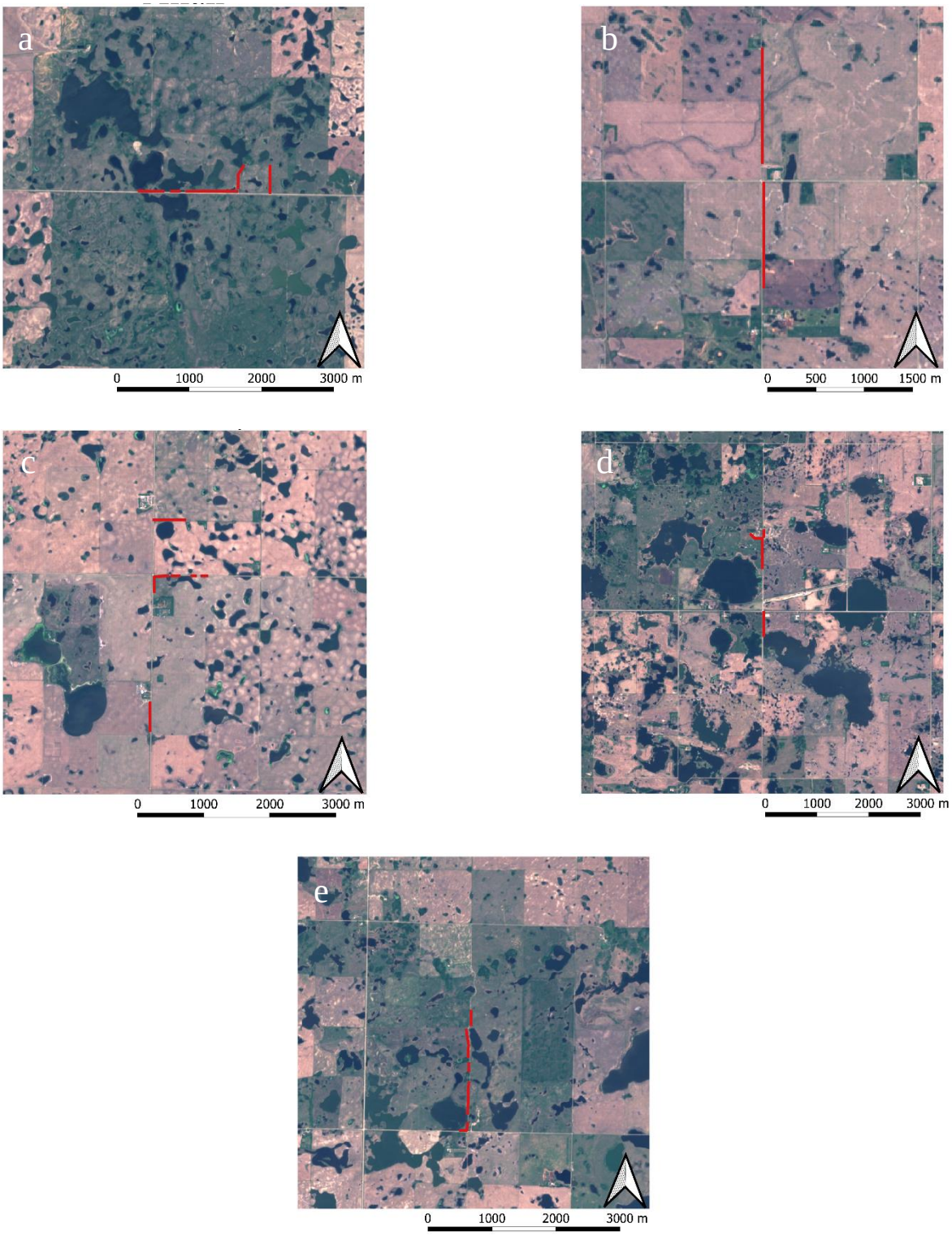

Figure 1.2. Maps of each study site. a) Allan, grassland-dominated; b) Burr; cropland-dominated c) Colonsay, cropland-dominated; d) Humboldt, dominated by cropland and herbaceous vegetation; e) St. Denis, grassland-dominated. Red line segments indicate the location of nest box transects. Contains modified Copernicus Sentinel data 2018, processed by ESA.

PREFACE TO CHAPTER 2

Intensive cropping practices can reduce the abundance of terrestrial invertebrates, resulting in reduction of prey for certain terrestrially-feeding insectivorous birds. However, the presence of non-crop habitats in agricultural landscapes can mitigate these effects by providing a source of invertebrate prey to birds breeding in cropland-dominated landscapes. Most studies have focused on the importance of terrestrial, non-crop habitat patches to grassland-breeding birds. Few have assessed the importance of aquatic habitats to birds breeding in agricultural landscapes. The primary objectives of this chapter were to assess 1) relative use of ponds and other habitats (habitat selection) by Tree Swallows breeding in prairie agroecosystems and 2) relationship of swallow foraging habitat selection to insect prey abundance or biomass in different habitats (land cover types, including herbaceous field margins, pond margins, grassland, and cropland). I acknowledge Thomas Ramsay for assistance in collection of insects and Dr. Lisha Berzins for her assistance in tagging and recapturing swallows.

CHAPTER 2: TREE SWALLOW FORAGING IN RELATION TO INSECTS IN PRAIRIE AGROECOSYSTEMS

2.1 ABSTRACT

On landscapes dominated by intensive crop cultivation, patches of non-crop habitat can benefit birds and insects by providing shelter, breeding habitat, and foraging areas. In the Prairie Pothole Region, wetland basins ("ponds," when flooded) may function as such critical habitat on landscapes dominated by cultivated cropland. Many aerial insectivores, especially swallows and martins (Family Hirundinidae), forage over water to capture insect prey. However, the degree to which ponds are selected by swallows relative to other habitats in agricultural landscapes remained unclear. Using GPS tags, I evaluated habitat selection and space use by breeding female Tree Swallows (*Tachycineta bicolor*) at sites with terrestrial land-use dominated by tame grass and grazing, herbaceous cover, and/or crop cultivation in southcentral Saskatchewan. I used sweep-net transects to assess abundance and biomass of flying insects in different habitat types (pond margins, herbaceous cover, grassland, and cropped fields) near swallow nests. GPS-tagged Tree Swallows selected for ponds relative to terrestrial habitats, on average. As expected for a central-place forager, swallows were increasingly selective for ponds at greater distance from nests. The distance at which swallows were detected from their nests was positively associated with daily mean temperature; probability of detection at nests was negatively associated with daily mean temperature and nestling age. I confirmed that cropped areas tend to have lower total insect abundance than ponds and grassy field margins on sites characterized by intensive cropping, while total abundance tended to be more uniform on grassland sites. Comparisons based on biomass suggested similar trends, but the difference between ponds and cropped uplands did not reach statistical significance in one year. Swallows tended to display strong selection for ponds relative to vegetation (primarily grass) as well as cropped areas, in slight contrast to prediction and patterns in sweep-net sampled insect abundance or biomass. I suggest that terrestrial sampling has not effectively captured prey "availability" to swallows given apparent selection for ponds over all terrestrial habitat. Nevertheless, these results underscore the importance of protecting and restoring prairie ponds and other aquatic habitats as critical foraging areas for swallows and possibly other aerial insectivores.

2.2 INTRODUCTION

Many species of North American-breeding aerial insectivorous birds (hereafter, "aerial insectivores") have experienced population declines in parts of their geographic ranges, though range-wide trends have stabilized recently in some species (Nebel et al. 2010, Smith et al. 2015, Michel et al. 2016, Sauer et al. 2017). The diversity of aerial insectivore life-histories and environmental requirements, combined with their collective reliance on flying insect prey, suggest a hypothesis that population trends of aerial insectivores may be related to changes in insect prey (Nebel et al. 2010). Expansion and intensification of arable agriculture (crop cultivation) have been implicated in population declines of insectivorous birds; the conversion of natural habitat to cultivated cropland (hereafter, "cropland") and intensive agricultural practices can cause local declines in invertebrate abundance and changes in invertebrate community composition – an apparent contributor to declines of farmland-associated birds (Boatman et al. 2004, Attwood et al. 2008, Nebel et al. 2010, Stanton et al. 2018). However, incorporation of terrestrial, non-crop habitats in agricultural landscapes has demonstrated potential to mitigate some adverse impacts of intensive cropping on insects and terrestrially-feeding insectivorous birds by providing shelter, breeding areas, and foraging habitat (e.g., Mineau and Mclaughlin 1996, Evans et al. 2003, but see Frenzel et al. 2016). Few have investigated the importance of aquatic habitats for insectivorous passerine birds in agricultural landscapes (Davies et al. 2016).

The Prairie Pothole Region (PPR) contains critical habitat for grassland birds as well as resident and migratory birds reliant on ponds of varying permanency (i.e., ephemeral to permanently flooded wetland basins) (Skagen et al. 2008, NABCI Canada 2012); however, the PPR also comprises productive agricultural land. In Canada, roughly 80% of cropland is concentrated in the Prairie Provinces (Saskatchewan, Alberta, and Manitoba), approximately half of which is located in Saskatchewan (Statistics Canada 2016). Consequently, the PPR has experienced an estimated loss of 40-70% of wetland basins in Canada (Government of Canada 1991) and an estimated 60-65% loss in the United States (Dahl 2014), primarily as a result of agricultural drainage and conversion to cropland. Drainage of ponds and conversion of wetland basins has continued, though accurate quantitative estimates of recent losses are hindered by the lack of a wetland "status and trends" monitoring program in Canada (Dahl and Watmough 2007, Watmough and Schmoll 2007, Dahl 2014). Temporary ponds in cropland appear to be most at risk for both degradation impacts (e.g., destruction of vegetated margins) as well as total loss

(Bartzen et al. 2010, Dahl 2014). Populations of some bird species reliant on semi-permanent prairie ponds have experienced population declines, underscoring the need for conservation and restoration of these habitats (NABCI Canada 2012).

All North American swallows and martins (Family Hirundinidae) forage over open water – including prairie ponds where ranges overlap (Elgin, pers. obs., Rodewald 2015). Tree Swallows (*Tachycineta bicolor*) have been especially well-documented to forage over water bodies to capture emerging aquatic insects (St. Louis et al. 1990, McCarty 1997). Aquatic insects are also prevalent in the diet of Tree Swallows nesting on sites with prairie ponds, with no differences in apparent diet composition from intensive cropping relative to tame grass and pasture (Michelson et al. 2018). Twining et al. (2018) reported that aquatic insect biomass, but not total or terrestrial insect biomass, had strong, positive effects on Tree Swallow fledging success. Likewise, supplementation of nestling Tree Swallow diets with omega-3 long-chain polyunsaturated fatty acids – typically more abundant in aquatic than terrestrial insects (Hixson et al. 2015, Twining et al. 2017) – enhanced nestling growth more than the quantity of food provisioned (Twining et al. 2016b). Collectively, these findings suggest that aquatic habitats, such as ponds, act as critical foraging areas and a source of nutrient-rich aquatic insects for Tree Swallows.

Importantly, breeding Tree Swallows, when foraging to provision nestlings, behave as central-place foragers (e.g., Orians and Pearson 1979, Schoener 1979); that is, swallows travel from a central place (the nest) to capture prey and return to the central place to feed nestlings. By extension from the marginal value theorem (Charnov 1976), central-place foraging theory predicts that foraging habitat patches located farther from the central place must provide greater energy returns (Orians and Pearson 1979). Therefore, selection for more profitable foraging habitat – that is, greater use of a given habitat than its availability on the landscape – should increase with distance from the central place (e.g., Patenaude-Monette et al. 2014, Heldbjerg et al. 2017). An increase in prey load size (and presumably energy content) has been associated with greater foraging distances in some swallows (Bryant and Turner 1982), in support of breeding swallows' behavior as central-place foragers.

I investigated whether prairie ponds function similarly to terrestrial, non-crop habitats for terrestrially-feeding birds, serving as foraging areas for breeding Tree Swallows in agricultural landscapes. I examined breeding female Tree Swallow habitat selection and space use on sites

characterized by cropland, grazed and un-grazed grassland, and/or herbaceous cover. I hypothesized that swallows would select for ponds as foraging areas, especially relative to cropped areas but less so relative to non-crop vegetation, because ponds and non-crop vegetation have greater densities of insect prey than cropland. Since breeding swallows behave as central-place foragers, I also predicted that selection for ponds would increase with distance from the central place (i.e., the nest box). Using sweep-net transects, I assessed insect abundance and biomass in field margins, pond margins, and characteristic uplands on sites with differing upland land cover and land use. I predicted that non-crop habitats (field margins and pond margins) harbor greater insect abundance and biomass than cropped uplands, but on sites dominated by grassland or herbaceous cover, different habitats (upland, field margin, or pond margin) would have similar insect abundance and biomass.

2.3 METHODS

2.3.1 Study Sites and Land Cover Classification

In 2017 and 2018, I monitored nest boxes at swallow colonies on four sites in southcentral Saskatchewan (all sites within ~75 km from each other). Sites were differentiated by dominant upland land use practices – grazed and un-grazed grassland (1 grassland site, "St. Denis"), cropping (2 cropland sites, "Burr" and "Colonsay"), or cropping alongside uplands seeded to un-grazed herbaceous cover (1 mixed site, "Humboldt"). Allan (a grassland site) was utilized for insect sampling in 2017 but excluded from all analyses in 2018 due to extreme (≳90%) nest failure unrelated to the study.

Land cover data for the study areas were derived from Copernicus Sentinel-2B satellite imagery with less than 10% cloud cover captured on 7 June 2018 (Copernicus Sentinel data 2018, processed by European Space Agency (ESA)). Supervised image classification in ArcMap (ArcGIS 10.5, ESRI) was used to classify a composite of the four 10 m spectral bands (B2 (490 nm), B3 (560 nm), B4 (665 nm) and B8 (842 nm)) into three classes: 1) "cropland" 2) "non-crop vegetation," which incorporated natural or semi-natural vegetation, including but not limited to trees, shrubs, and herbaceous cover, and 3) "ponds," which incorporated open water. Bare ground and developed areas (primarily roads) tend to have similar flying insect densities to cropped areas (Elgin, pers. obs.), so these land cover classes were combined. Cropland can be bare during the early nestling period in this region. This grouping also enabled simultaneous use of all data in a single habitat use model, which reduces the likelihood of spurious apparent

habitat selection due to spatiotemporal autocorrelation (e.g., perching in trees) and rarity on the landscape (e.g., cropped areas on the grassland site and non-crop vegetation on cropland sites). The road segment of the National Road Network shapefile for Saskatchewan (Statistics Canada 2018) was used to classify 10 m on each road as "cropland" bounded on both sides by 10 m of "non-crop vegetation," representative of grassy road margins. Due to slight inaccuracies in the roads shapefile, the road additions were not allowed to overlap ponds in the land cover raster. Pond areas were partially ground-truthed by mapping pond perimeters with a handheld GPS unit (Garmin GPSMAP 64ST, Garmin Ltd., Olathe, Kansas, USA) on two study sites from 30 May to 5 June 2018.

2.3.2 Tree Swallow Nest Monitoring

Beginning in May 2018, nest boxes were checked for occupancy every 2-3 days based on nest building. Occupied boxes were checked approximately every other day until clutch completion (determined as three consecutive days with no additional laying). Nests with complete clutches were checked for hatching near the end of the incubation period (11 days following clutch completion at St. Denis or 12 days following clutch completion at all other sites). The date when the first nestling was observed was assigned as the hatch date (day zero post-hatching or day zero of nestling life); if hatch dates were not directly observed, these were estimated post-hatch based on several factors including prior "starring" of eggs (early pipping presumed to occur on day prior to hatching), nestling size and feather tract development, and number of nestlings hatched.

2.3.3 GPS Instrumentation and Sampling

I attached GPS tags (Lotek PinPoint-10, Lotek Wireless Inc, Newmarket, Ontario, Canada; attachment mass 1.2 g, ≲6% body mass) to 25 adult female swallows captured at the nest box when nestlings were 5-8 days old (13-26 June 2018). Prior to tag attachment, females were weighed to the nearest 0.25 g using a Pesola spring scale. I attached tags using a leg-loop harness (Rappole and Tipton 1991) of 0.5 mm Stretch Magic jewelry cord (Pepperell Braiding Company, Pepperell, Massachusetts, USA), as described by Streby et al. (2015). No tags failed nor were any lost to harness failure using this method. Tags were pre-programmed to attempt a GPS fix (*SWIFT*-fix, nominal horizontal accuracy ± 20 m) at 0500 local time on the day following attachment and subsequently attempt a fix every ten minutes until 2200 local time. Tagged

females were recaptured at the nest box, and tags were removed. Using handheld GPS units (Garmin GPSMAP 64ST), I obtained the coordinates of the nest box where tagged females were captured. Tags were recovered from eight females at St. Denis, six females at Colonsay, six females at Humboldt, and four females at Burr (n = 24); one tagged female was not recaptured.

2.3.4 Terrestrial Sweep-net Sampling and Taxonomic Identification of Insects

In 2017 and 2018, standardized sweep-netting was conducted on transects using conical nets (Ward's Professional Insect Net, VWR cat # 470018-488). In 2017, sweep-netting was conducted just prior to the period of peak hatching (7-8 June, 2017, "early" sweep period) and peak nestling rearing (19 June, 2017, "late" sweep period). In 2018, sweep-netting was conducted on each site during the period of peak hatching (9-14 June 2018). Sweep-net samples from the Humboldt site in 2017 could not be assigned to clear habitat types due to partial conversion of previously cropped areas to herbaceous cover; hence, these data were not formally analyzed. In 2018, the Humboldt site was treated as two sub-sites, one with uplands dominated by herbaceous cover ("Humboldt Grass"), the other with uplands characterized by cropland ("Humboldt Crop"). On each site or sub-site, I conducted the following sweep-net transects: four 50 or 25 m transects, each separated by at least 50 m, in different habitat types: 1) uplands representative of the site (i.e., in tame grass, herbaceous cover, or cropped fields), 2) pond margins, within approximately 2 m of ponds (one transect per pond), and 3) field margins of non-crop vegetation (primarily grassy road margins). In 2017, effective sample sizes (resulting from the pooling of samples or summing of data from the same upland fields) were as follows: on cropland sites, 8 field margins, 4 uplands, and 8 pond margins per sweep period and on grassland sites, 8 field margins, 4 uplands, and 8 pond margins per sweep period. In 2018, effective sample sizes were as follows: on cropland sites, 12 field margins, 6 uplands, and 12 pond margins and on grassland sites, 8 field margins, 5 uplands, and 8 pond margins. Samples were stored in sealed plastic bags, on ice, in the field and subsequently stored at -20°C (2017) or -80°C (2018).

Samples from both years were thawed and identified to order according to dichotomous keys in Triplehorn and Johnson (2005). Diptera and Odonata were further sorted to suborder. Nematoceran Diptera, Odonata, and Trichoptera were considered aquatic in origin. Brachyceran Diptera were considered to represent primarily terrestrial and some aquatic taxa. Remaining taxa

were, collectively, considered primarily terrestrial. Damselflies (Odonata: Zygoptera) are a regular component of swallow diets on these sites (Elgin, pers. obs.). However, dragonflies (Odonata: Anisoptera) are unusual in swallow diets (Quinney and Ankney 1985, McCarty and Winkler 1999b), and few were captured (one individual in 2017, none in 2018). Therefore, dragonflies, thrips (Thysanoptera, all ≲1mm), wingless individuals (e.g., nymphs, larvae), and arachnids were excluded from analyses, as these taxa are typically minor components of swallow diets (Winkler et al. 2011) or were incompletely sampled. Individuals unidentifiable to order/suborder (degraded samples) and one Hymenopteran which was lost (n = 10 individual insects from 7 transects in 2017) were also excluded. Samples were freeze-dried for a minimum of 24 h, until dry, and subsequently weighed to obtain dry biomass to the nearest 0.1 mg using an analytical balance (Ohaus Explorer Pro, model EP114C, Ohaus Corporation, Pine Brook, NJ, USA).

2.3.5 Data Processing and Analyses

2.3.5.1 Tree Swallow Habitat Selection

All data processing and analyses were conducted in R (R Core Team 2018). GPS fixes with horizontal dilution of precision (HDOP) values >5 were removed from the sample to increase the accuracy of habitat assignment and calculation of distance from the nest box (hereafter, "distance from nest"). Distance from nest was calculated and assigned to each GPS fix using the "pointDistance" function from the raster package (Hijmans 2017). Fixes obtained during apparent roosting were removed for one female detected >3 km from the nest from approximately 2130 to 2200 local time. After filtering, 2388 GPS fixes were considered usable; median fix count per female was 100 (range: 95-102).

To assess females' foraging habitat use, a resource selection function (RSF) approach was used under a use-availability design (Boyce et al. 2002, Manly et al. 2002). Habitat selection analyses focused on third-order habitat selection (i.e., habitat selection within a presumed daily home range) (Johnson 1980). For analyses of habitat selection, all GPS fixes within 20 m (nominal horizontal accuracy for the GPS tags) of nests were removed. GPS fixes were re-projected to match the projection of the land cover raster using function "spTransform" (Pebesma and Bivand 2005). A 100% minimum convex polygon (MCP) surrounding GPS fixes for each female was generated using the package adehabitatHR (Calenge 2006). For each female, 10,000 random points were generated within the MCP to constitute a sample of

availability. A habitat class (cropland, non-crop vegetation, or pond) was assigned to each of the remaining GPS fixes (i.e., those remaining after filtering on HDOP and distance from nest; n = 1592, median by female = 64 (range: 43–88)) and the random points according to the land cover raster using the "extract" function from the raster package (Hijmans 2017). After re-projection of random points, distance (m) from the respective nest was calculated and assigned to each random point using the "pointDistance" function (Pebesma and Bivand 2005, Hijmans 2017). Random points <20 m from the respective nest were removed.

Mixed-effects logistic regression in lme4 (Bates et al. 2015) was used to model the probability points would be categorized as used (GPS fixes = 1) or available (random points = 0). Fixed effects included habitat ("cropland," "non-crop vegetation," or "pond"), distance from nest, and their interaction. A random intercept term for female identity was included to account for varying ratios of use and availability points across swallows. To account for individual variation in selection, random coefficients (uncorrelated with random intercepts) for habitat, distance from nest, and their interaction were also included (Gillies et al. 2006). Type-II Wald Chi-square tests were conducted as a test of fixed effect significance via package car (Fox and Weisberg 2019). Model-estimated marginal means for the trend in distance from nest (on the logit scale) by habitat class were compared using Z-tests with Tukey-adjusted p-values via the "emtrends" function from package emmeans (Lenth 2018). To assess whether the interpretation of habitat selection was dependent on the interaction term, a main effects only model was also fit to these data, dropping only the interaction between distance from nest and habitat and the corresponding random coefficient term. Model-estimated log-odds ratios between habitat classes were tested using Z-tests with Tukey-adjusted p-values in package emmeans (Lenth 2018).

2.3.5.2 Tree Swallow Nest Attendance and Space Use

Two modelling approaches were used to assess effects on females' space use, presumably reflective of foraging activity. The first approach considered the probability that females were detected either near or away from the nest. When females were within 20 m of the nest, they were considered to be at the nest. Mixed-effects logistic regression was used to model the probability that females would be at the nest (1) or away (0). The model included effects of daily mean temperature, daily total precipitation, maximum daily wind gust speed ("low" ≤30 km/h; "high" >30 km/h), site, nestling age (days), and a random intercept term for female identity. The second approach considered the distance from nest that females were detected, for fixes >20 m

from nests (i.e., the female was not at the nest). A mixed-effect model with gamma-distributed errors and an inverse-link function was used to model effects on distances from the nest. The model included effects of daily mean temperature, daily total precipitation, maximum daily wind gust speed, site, nestling age, and a random intercept term for female identity. Though females were tagged at similar stages during brood rearing, nestling age was incorporated to account for changes in foraging effort during nestling growth. I detected moderate collinearity and confounding of nestling age with mean daily temperature (nestlings on day 6 of life experienced high temperatures, while nestlings on day 9 of life experienced low temperatures); effects and statistical significance for nestling age in the distance-based model should be interpreted with caution. For both approaches, Type II Wald Chi-square tests were conducted as a test of fixed effect significance via package car (Fox and Weisberg 2019).

Daily mean temperature (°C), daily maximum wind gust speeds (km/h), and daily precipitation (mm) were obtained from local weather stations operated by Environment and Climate Change Canada in Watrous (WMO ID 71511) or Saskatoon (WMO ID 71496). When data were available for both stations, the mean was used in analyses. Because only maximum wind gust speeds >30 km/h are reported, daily maximum wind gust speeds ≤30 km/h were recoded as "Low" and >30 km/h as "High." In the one instance of only one station exceeding the threshold, the higher value was used.

In all analyses, the threshold for statistical significance (α) was set at 0.05. To summarize the distance from nests of GPS fixes, I used R "type 7" quantiles (R Core Team 2018). I used packages ggplot2 (Wickham 2009) and effects (Fox 2003, Fox and Weisberg 2018, 2019) to visualize data and model predictions, and I used QGIS to generate maps of GPS fixes (QGIS Development Team 2018).

2.3.5.3 Terrestrial Sweep-Net Insect Abundance and Biomass

I used a different sweep-net sampling strategy in 2017 and 2018; therefore, sweep-net data from each year were analyzed separately. To assess patterns in sweep-net sampled insect abundance, function "glmer.nb" from package lme4 (Bates et al. 2015) was used to fit negative binomial mixed-effects models to insect count data. Models incorporated fixed effects of habitat type (upland, pond margin, or field margin), site type (cropland-dominated or grassland-/herbaceous- dominated), sweep period (early or late, 2017 only), and all possible interactions, with a random intercept for site and an offset term for the natural log of the transect

distance. Offset terms were incorporated to account for different transect distances. The sum of counts from the same upland fields was used; hence, transect distance for these pooled counts was considered 100 m. For one Brachyceran sample (2017), count data were estimated using a linear model incorporating Brachyceran counts as a response and Brachyceran dry biomass as predictor. For four degraded Nematoceran samples (2018), counts were estimated using a general linear model incorporating Nematoceran counts as a response and Nematoceran dry biomass as predictor. Type II Wald Chi-square tests were conducted as a test of fixed effect significance via package car (Fox and Weisberg 2019). Model-estimated marginal means were compared using Z-tests with Tukey-adjusted p-values via package emmeans (Lenth 2018).

To assess patterns in sweep-net sampled insect biomass, package lme4 (Bates et al. 2015) was used to fit linear mixed-effects models to natural log-plus-one transformed (2017) or natural log-transformed biomass data (2018). Models incorporated fixed effects of habitat type (upland, pond margin, or field margin), site type (cropland-dominated or grassland-/herbaceous-dominated), sweep period (early or late, 2017 only), and all possible interactions, with a random intercept for site and an offset term for the natural log of the transect distance. Again, the sum of biomass from the same upland fields was used, and transect distance for these pooled samples was considered to be 100 m. For the model of 2017 biomass data, the homogeneity of variance assumption was not satisfied; therefore, p-values from models and model-estimated marginal means for 2017 biomass data should be interpreted with caution. Statistical significance was assessed using Type II Wald F-tests with the Kenward-Roger degrees of freedom approximation via package car (Fox and Weisberg 2019). Model-estimated marginal means were compared using t-tests (Kenward-Roger method) and Tukey-adjusted p-values via package emmeans (Lenth 2018).

2.4 RESULTS

2.4.1 Summary of GPS Data

Of the 2388 GPS fixes utilized, 33% (n = 796/2388) were within 20 m of the nest, and 67% (1592/2388) were away from nests. The maximum distance from nest was 2525 m (HDOP = 0.8, Humboldt site). Of the 1592 fixes farther than 20 m from nests (“used” habitat, across all swallows), 32.8% were located above cropland, 40.1% were above non-crop vegetation, and 27.1% were above ponds. Of the random points (“available” habitat) farther than 20 m from nests (across all swallows), 41.6% were above cropland, 39.5% were above non-crop vegetation,

and 18.9% were above ponds. However, habitat use and availability differed across swallows and varied by distance from the nest. Table 2.1 displays the number of tagged females represented on each site and the land cover characterization of each study site utilized in 2018. Percentiles of the calculated distance from nest for all fixes and fixes assumed to be away from the box are presented in Table 2.2.

2.4.2 Tree Swallow Habitat Selection

Based on the RSF, there was a statistically significant interaction effect between habitat type and distance from the nest (χ^2 (2) = 29.52, $p < 0.001$, Table A1, A2). Comparison of model-estimated slopes (on the logit scale) suggested that the interaction effect was driven by increasing selection for ponds relative to other habitat classes at greater distances from the nest box (Table 2.3, Figure 2.1, 2.2). While the RSF suggested a decline in the relative probability of use for all habitats at greater distances, the slope of decline was steeper for terrestrial habitats than for ponds. An RSF incorporating only main effects did not alter qualitative inferences regarding foraging habitat selection; the log odds-ratio for selection of ponds relative to other habitats was >0, with no statistically significant difference between cropland and non-crop vegetation (Table A3).

2.4.3 Weather, Nestling Age, and Site Effects on Tree Swallow Space Use

I found statistically significant effects of daily mean temperature (χ^2 (1) = 26.50, $p < 0.001$) and nestling age (χ^2 (1) = 7.12, $p = 0.008$, Table A4, A5) on probability of females being detected at the nest box. Model-predicted probability of detecting females at nests decreased as daily mean temperature increased or as nestlings grew older (Figure A1). Effects of precipitation, wind gust speed, and site were not statistically significant ($p > 0.05$).

I also found a significant effect of daily mean temperature on distance of detections from the nest box (χ^2 (1) = 5.88, $p = 0.015$, Table A6, A7). Distance of detections from the nest box tended to increase as daily mean temperature increased (Figure A2). Effects of precipitation, wind gust speed, site, and nestling age were not statistically significant ($p > 0.05$).

2.4.4 Terrestrial Sweep-net Insect Abundance and Biomass

The interaction of habitat, site type, and sweep period on 2017 sweep-net sampled insect abundance was statistically significant (χ^2 (2) = 13.87, $p < 0.001$, Table A8, A9, Figure 2.3). Post-hoc comparisons suggested that a) cropped uplands had lower insect abundance than field margins or pond

margins on cropland sites, regardless of sweep period, b) during the early sweep period, cropped uplands had lower insect abundance than habitats on grassland sites, and c) field margins on grassland sites had greater insect abundance during the early sweep period than did field margins or uplands on grassland sites during late sweeps (Table A10).

The interaction of habitat and site type on 2018 sweep-net sampled insect abundance was statistically significant (χ^2 (2) = 15.97, $p < 0.001$, Table A11, A12, Figure 2.4). Post-hoc comparisons indicated that cropped uplands had lower insect abundance than all other habitat and site type combinations (Table A13).

The interaction of habitat, site type, and sweep period on 2017 sweep-net sampled insect biomass was not statistically significant ($F_{2, 66} = 0.50$, $p = 0.61$, Table A14, A15); however, the interaction of habitat and site type on total sweep-net sampled insect biomass was statistically significant ($F_{2, 66} = 30.43$, $p < 0.001$, Figure 2.5), as was the main effect of sweep period ($F_{1, 66} = 8.26$, $p = 0.01$). All non-significant interactions were dropped prior to post-hoc testing (Table A16). Post-hoc comparisons suggested that cropped uplands had lower insect biomass than all other habitat types and that, on cropland sites, field margins had greater insect biomass than pond margins (Table A17). Sweep-net sampled insect biomass was greater in the late period than in the early period (Table A18).

The interaction of habitat and site type on 2018 sweep-net sampled insect biomass was statistically significant ($F_{2, 42.02} = 5.01$, $p = 0.01$, Table A19, A20, Figure 2.6). Post-hoc comparisons indicated that field margins on cropland sites had greater insect biomass than did cropped uplands (Table A21). Table 2.4 provides a summary of sorted insect abundance and biomass across years.

2.5 DISCUSSION

2.5.1 Swallow Selection for Ponds: Increasing Selectivity with Travelling Distance

Breeding female Tree Swallows selected for prairie ponds over terrestrial habitats and increased their selection for ponds with increasing distance from the nest. The latter pattern is consistent with central-place foraging theory; when swallows travel farther, they appear to be increasingly selective for more profitable foraging habitats (presumably, ponds with greater emergent insect densities). This pattern may represent additional evidence that swallows'

selection for ponds is directly related to foraging efficiency; it is unclear why swallows would travel farther than necessary to reach water except to exploit more profitable foraging patches. These results are consistent with several recent studies confirming that central-place foraging birds tend not only to increase prey/food load size with greater foraging distances, but increase habitat selectivity at greater distances from the central place, presumably to take advantage of concentrations of prey/food (e.g., Patenaude-Monette et al. 2014, Heldbjerg et al. 2017). Previous studies have also found that Tree Swallows capitalize on concentrations of emerging aquatic insects in "preference" to foraging over terrestrial habitats (St. Louis et al. 1990, McCarty 1997).

While Tree Swallows appear to be selective for prairie ponds, RSFs did not suggest differential selection between other habitat types. Contrary to prediction, I did not detect differential selection for vegetation relative to the class of cropland; rather, both RSF approaches suggested that swallows select for ponds, with less difference between other habitats. My results likely underestimate the use of ponds relative to terrestrial habitats, given the intermittent nature of spatiotemporal sampling (one GPS fix every ten minutes). Swallows travelling to and from ponds will be detected over terrestrial habitats, but I suspect such errors would be similar across land cover types. Nevertheless, if swallows' use of ponds is related to intake of emerging aquatic insects, these results are consistent with previous findings that the predominance of aquatic insects in swallow diets is not directly affected by intensive cropping relative to tame grass and pasture, when ponds are present (Michelson et al. 2018). This being the case, swallow selection for ponds over most terrestrial habitat may align with the apparent differential importance of aquatic insects in driving Tree Swallow reproductive output (Twining et al. 2018).

2.5.2 Drivers of Swallow Space Use

I also found that Tree Swallows' presumed foraging activity, based on females being away from or farther from the nest box, increased with greater ambient temperatures and nestling age. These patterns likely reflect the importance of ambient temperature as a driver of Tree Swallow foraging activity, with important consequences for swallow reproductive output; increased temperature can drive aquatic insect emergence and insect flight and therefore, availability to Tree Swallows (e.g., Winkler et al. 2013). Importantly, because I sampled only female swallows, caution should be taken in extrapolating these patterns across the sexes.

Temperature-dependent activity may reflect, in part, increased brooding of nestlings in colder temperatures, since female swallows are primarily or solely responsible for brooding nestlings(Winkler et al. 2011). While statistically significant effects of precipitation or wind gust speed were not detected, power to detect such effects was limited by minimal variation in precipitation and wind gust speed over the study period.

I did not detect site effects on either the probability of detection near the nest or distance of detections from the nests, suggesting that females were not consistently spending more time away from nests on any given site. The lack of site effects is not particularly surprising considering the RSF results. Given that ponds are available, female swallows select for ponds over cropped or vegetated areas, and none of these swallow colonies was truly "pond-limited" (Table 2.1). Further, given that swallows behave as central place foragers, they will presumably forage closer to nests, only travelling farther when the benefit of doing so (increased prey intake/capture) is equal to or, more likely, outweighs the energetic cost of travelling. This suggests a cost of foraging habitat limitation on Tree Swallows (e.g., loss of productive aquatic habitat). While some benefits may be gleaned by swallows nesting in more "natural" habitats, the weight of evidence suggests that productive ponds are more critical for breeding Tree Swallows than terrestrial landscape structure. I acknowledge that tagging itself could affect foraging behavior (e.g., duration of foraging) (Bodey et al. 2017), despite that I observed minimal or no effect on female mass (data not shown). Still, I suggest that such effects would be similar across swallows, and other effects on trip duration would likely be compounded, rather than reduced, by tagging.

2.5.3 Insect Abundance and Biomass: Habitat Differences

I found that sweep-net sampled insect abundance on cropland sites tended to be greater in field margins and pond margins than in cropped uplands. Biomass results suggested similar, if less consistent, trends. The data and models indicate a consistent pattern: on cropland sites, cropped uplands tended to have lower sweep-net sampled insect abundance than field margins and pond margins. Given that cropped and grassland uplands also tended to differ in insect abundance, this suggests that crop cultivation drives changes in abundance of sweep-net sampled insects among these habitats. However, it remains unclear precisely which factors are driving this effect – vegetation structure, loss of suitable habitat, and insect foraging are among possible

contributors (Andow 1991, Grüebler et al. 2008). Differences in apparent quantity of insects as based on biomass and abundance have also been reported in previous studies of Diptera (common prey in Tree Swallow diets) which suggest that intensive cropping may be associated with changes in temporal patterns of abundance, but not necessarily biomass of this taxon (Paquette et al. 2013, Bellavance et al. 2018). It remains unclear whether total insect biomass or abundance represents a more accurate measure of prey availability to swallows, if either measure is representative at all.

I suggest that there are site and year effects, as well as temporal trends, in insect abundance and/or biomass representing critical differences which I was not able to directly address due to sampling strategy. For example, abundance and biomass data from 2018 suggest that the Humboldt site has lower insect densities in pond margins than ponds on other sites. The primary accessible ponds for sweep-net sampling at Humboldt are more accurately described as shallow lakes which have flooded into previously cropped areas. These larger water bodies tend to have lower insect densities than semi-permanent ponds on this site, and swallows are not typically observed foraging in these areas (Elgin, pers. obs.). Anecdotally, females at the Humboldt site tended to exhibit some of the greatest travelling distances, sometimes visiting smaller, presumably more productive ponds, despite the proximity of these large water bodies to their nests. Given that Humboldt was excluded from analyses of 2017 insect sampling, this may also contribute to differences across years in statistical significance of habitat comparisons.

2.5.4 Insect Distribution and Tree Swallow Habitat Selection

Patterns in sweep-net sampled insect abundance and biomass appear generally consistent with lower insect abundance in cropped fields. However, these patterns do not support the hypothesis that swallows are utilizing ponds solely because they offer greater insect densities than other habitats. Despite female swallows' selection for ponds over non-crop vegetation, I did not detect any consistent difference between field margins, grassland uplands, and pond margins for sweep-net sampled insect abundance or biomass. I suggest this is, in part, because terrestrial sweep-net sampling does not accurately reflect true availability of insect prey to Tree Swallows. Tree Swallows likely have reduced access to insects sheltering in vegetation, which are captured in sweep-netting, whereas insects emerging from ponds are readily captured by swallows. Studies of bats suggest that prey availability is, at minimum, a function of detectability,

accessibility, and abundance. While dense vegetation tends to harbor greater concentrations of insect prey, it appears to reduce prey accessibility and detectability to aerial insectivorous species (Rainho et al. 2010, Almenar et al. 2013). Swallows are also known to forage low over water, taking insects just below or actively emerging from pond surfaces, but will also take advantage of ephemeral clusters of insects at higher altitudes (up to >600 m) (Cohen and Dymerski 1986, McCarty 1997, McCarty and Winkler 1999b, Dreelin et al. 2018). Hence, the spatiotemporal distribution of insects taken by foraging Tree Swallows may not be reflected in terrestrial sweep-net sampling.

Sweep-net sampling of pond margins also did not capture the emergence of aquatic insects. These data suggest that primarily aquatic insects, especially Nematoceran Diptera, were concentrated in grassy field margins or grassland (Table 2.4). Considering that Tree Swallows, both on these sites and more generally, tend to consume primarily aquatic insects (Winkler et al. 2011, Michelson et al. 2018), I speculate that swallows select for ponds to take advantage of actively emerging aquatic insects as more easily captured and/or higher quality prey. However, I cannot rule out the possibility that swallows forage near ponds because they are selective for Brachyceran Diptera, as reported by McCarty and Winkler (1999a), which sweep-net data suggest are most abundant near pond margins. Future studies should consider the use of emergence traps alongside terrestrial sampling when assessing prey availability to swallows, with an understanding that aquatic habitats (e.g., individual ponds) are not equal in terms of insect emergence.

2.5.5 Conclusions

I found that while croplands tended to harbor lower sweep-net sampled insect abundance than field and pond margins, Tree Swallows selected for ponds over all terrestrial habitats and were increasingly selective at greater distances from their nests. I caution against overinterpreting the lack of difference for swallows' terrestrial habitat selection, as it remains unclear how swallows behave in the absence of ponds near nesting locations. Still, results here suggest that, for Tree Swallows, terrestrial non-crop habitats do not serve as "replacement" for ponds in agroecosystems. Tree Swallows also appear to consistently behave as central-place foragers, suggesting there may be limits to compensatory foraging effort; at some distance from the nest, the energetic cost of travelling farther will outweigh benefits gleaned by increasing

selection for more profitable foraging areas (for swallows, aquatic habitat). Collectively, these results underscore the importance of conserving aquatic habitats, such as prairie ponds in agricultural landscapes, to provide important foraging areas for breeding Tree Swallows, and likely, other aerial insectivores.

TABLES AND FIGURES

Table 2.1. Summary of GPS-tagging sample sizes and land cover on study sites in June 2018 based on land cover classification of Sentinel-2B imagery (derived from modified Copernicus Sentinel data 2018, processed by European Space Agency). Land cover values represent percentage of raster cell count within a 1000 m buffer around Tree Swallow nest boxes.

Site	Cropland	Non-crop Vegetation	Ponds	No. Females Tracked
Colonsay	81%	8%	10%	6
Burr	77%	19%	4%	4
Humboldt	39%	29%	32%	6
St. Denis	15%	67%	18%	8

Table 2.2. Summary of the distance from nest of female swallow GPS fixes. Percentiles were calculated on the basis of all 2388 fixes ("All Fixes") or the 1592 fixes considered to be away (>20 m) from the nest box ("Fixes Away from Nests").

Percentile	All Fixes	Fixes Away from Nests
25%	9 m	78 m
50%	78 m	180 m
75%	263 m	371 m
90%	483 m	582 m
95%	705 m	874 m
99%	1358 m	1511 m

Table 2.3. Contrasts of model-estimated trends in distance from the nest by habitat type. Contrasts represent a comparison of the slope (on the logit scale) of the covariate trend (distance from box) for each habitat class derived from the resource selection function. SE, standard error.

Contrast	Estimate	SE	Z-ratio	p
Non-crop Vegetation – Cropland	-0.19	0.90	-0.21	0.98
Pond – Cropland	6.16	1.32	4.66	<0.001
Pond – Non-crop Vegetation	6.35	1.19	5.34	<0.001

Table 2.4. Summary table of sweep-net sampled insect abundance and biomass by site type (cropland- or grassland/herbaceous-dominated) and habitat (grassy field "margins", "uplands", or "pond" margins) across years. Values represent arithmetic mean distance-corrected abundance or biomass (individuals/m or mg/m) across transects and sweep periods, as applicable, plus or minus one standard deviation. Four sites were utilized in 2017, and five sites or sub-sites were utilized in 2018.

	Cropland Sites			Grassland Sites		
2017 Abundance	Margin (n = 16)	Upland (n = 8)	Pond (n = 16)	Margin (n = 16)	Upland (n = 8)	Pond (n = 16)
Aquatic Taxa	1.0 ± 0.8	0.0 ± 0.1	0.4 ± 0.5	1.0 ± 1.7	0.9 ± 1.2	0.3 ± 0.2
Brachyceran Diptera	0.5 ± 0.6	0.1 ± 0.1	0.9 ± 1.2	0.1 ± 0.1	0.1 ± 0.1	0.5 ± 0.5
Other Taxa	0.4 ± 0.4	0.0 ± 0.0	0.4 ± 0.7	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.3
Total	1.9 ± 1.1	0.1 ± 0.2	1.7 ± 2.2	1.2 ± 1.7	1.1 ± 1.3	1.1 ± 0.8
2018 Abundance	Margin (n = 12)	Upland (n = 6)	Pond (n = 12)	Margin (n = 8)	Upland (n = 5)	Pond (n = 8)
Aquatic Taxa	6.0 ± 11.3	0.3 ± 0.3	0.5 ± 0.6	2.7 ± 1.6	4.7 ± 6.1	0.5 ± 0.5
Brachyceran Diptera	0.3 ± 0.2	0.1 ± 0.1	0.9 ± 0.8	0.1 ± 0.1	0.1 ± 0.1	1.4 ± 1.9
Other Taxa	0.4 ± 0.5	0.0 ± 0.0	0.3 ± 0.5	0.3 ± 0.2	0.3 ± 0.3	2.0 ± 2.7
Total	6.7 ± 11.6	0.4 ± 0.4	1.7 ± 1.7	3.1 ± 1.5	5.1 ± 6.0	3.9 ± 4.6
2017 Biomass	Margin (n = 16)	Upland (n = 8)	Pond (n = 16)	Margin (n = 16)	Upland (n = 8)	Pond (n = 16)
Aquatic Taxa	5.7 ± 4.3	0.1 ± 0.1	2.0 ± 3.0	1.1 ± 0.9	1.5 ± 1.0	1.6 ± 1.8
Brachyceran Diptera	1.1 ± 1.4	0.2 ± 0.3	2.0 ± 2.5	0.2 ± 0.2	0.2 ± 0.2	1.5 ± 2.1
Other Taxa	1.7 ± 1.9	0.0 ± 0.0	1.0 ± 1.3	0.6 ± 1.7	0.9 ± 0.7	0.7 ± 0.7
Total	8.5 ± 3.4	0.3 ± 0.3	5.0 ± 4.7	1.9 ± 1.8	2.6 ± 1.4	3.9 ± 3.1
2018 Biomass	Margin (n = 12)	Upland (n = 6)	Pond (n = 12)	Margin (n = 8)	Upland (n = 5)	Pond (n = 8)
Aquatic Taxa	12.1 ± 27.1	0.3 ± 0.3	0.7 ± 0.9	3.1 ± 1.8	6.1 ± 6.8	1.0 ± 1.2
Brachyceran Diptera	0.7 ± 0.6	0.2 ± 0.1	2.0 ± 2.0	0.4 ± 0.4	0.3 ± 0.2	3.5 ± 5
Other Taxa	1.8 ± 2.3	0.1 ± 0.1	0.9 ± 1.6	0.9 ± 0.6	0.6 ± 0.7	2.8 ± 3.8
Total	14.5 ± 27.6	0.5 ± 0.5	3.6 ± 4.1	4.3 ± 1.4	7.0 ± 6.7	7.3 ± 9.2

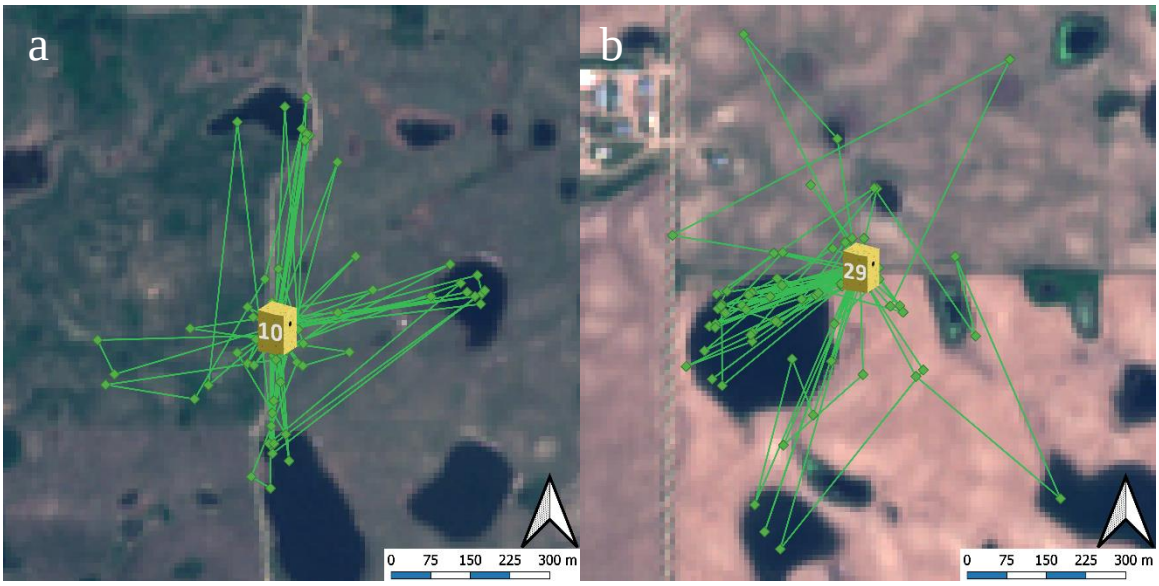

Figure 2.1. Locational fixes for two breeding female Tree Swallows overlain on Sentinel-2B true color imagery (contains modified Copernicus Sentinel Data 2018, processed by ESA). Left (a), fixes from a swallow breeding at St. Denis (grassland-dominated site). Right (b), fixes from a swallow breeding at Colonsay (cropland-dominated site). Green diamonds represent GPS fixes, with green lines connecting consecutive fixes.

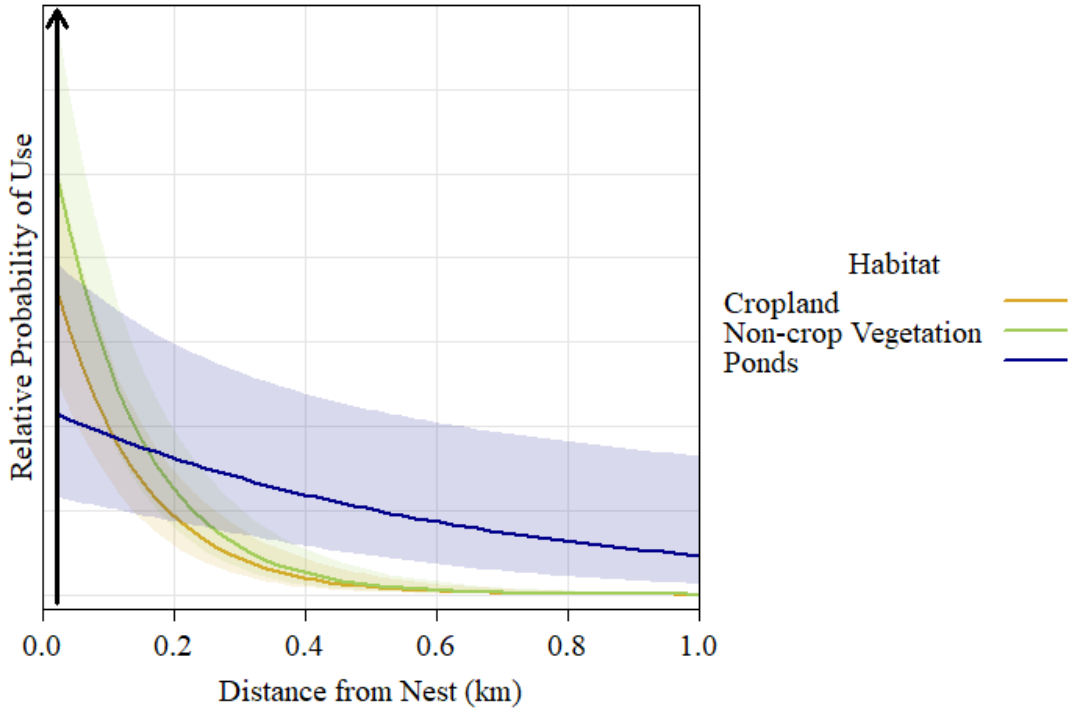

Figure 2.2. Model predictions from the resource selection function. Relative probability of use (given equal availability) is indicated along the y-axis and distance from the nest on the x-axis. Habitat types (cropland, non-crop vegetation, or ponds) are color-coded, and shaded areas represent 95% confidence intervals. The x-axis has been truncated at 1 km.

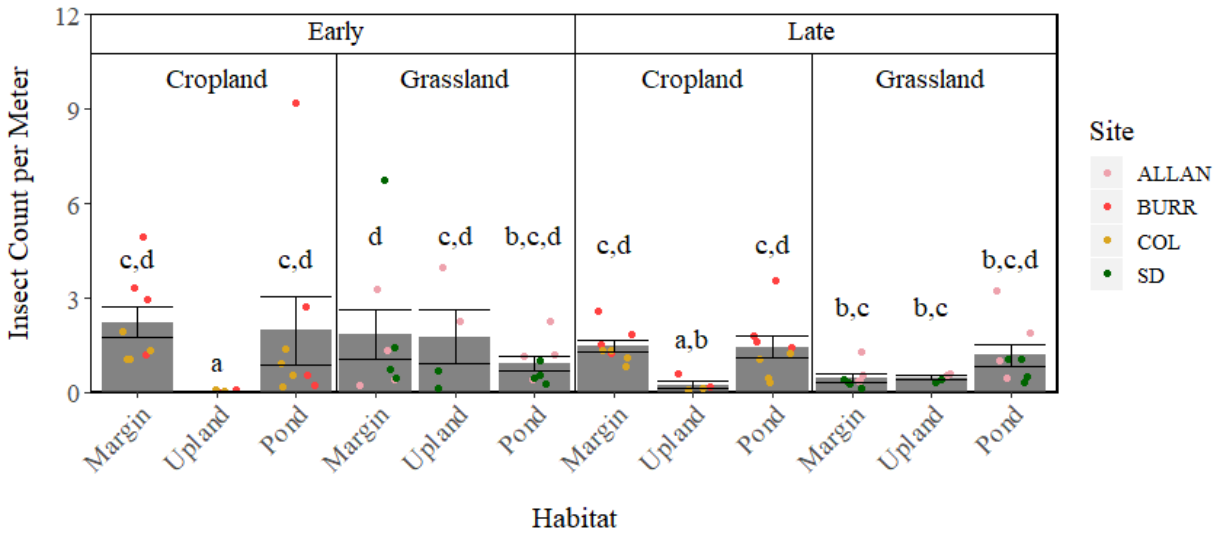

Figure 2.3. Bar chart of arithmetic mean insect count/m by site type (cropland- or grassland-dominated), habitat (grassy field "margins," "uplands," or "pond" margins) and sweep period (early or late) in 2017. Error bars represent one standard error of the mean. Datapoints are color-coded by site (Col, Colonsay; SD, St. Denis). Significant pairwise comparisons of model-estimated marginal means ($p < 0.05$) are indicated by differing letters.

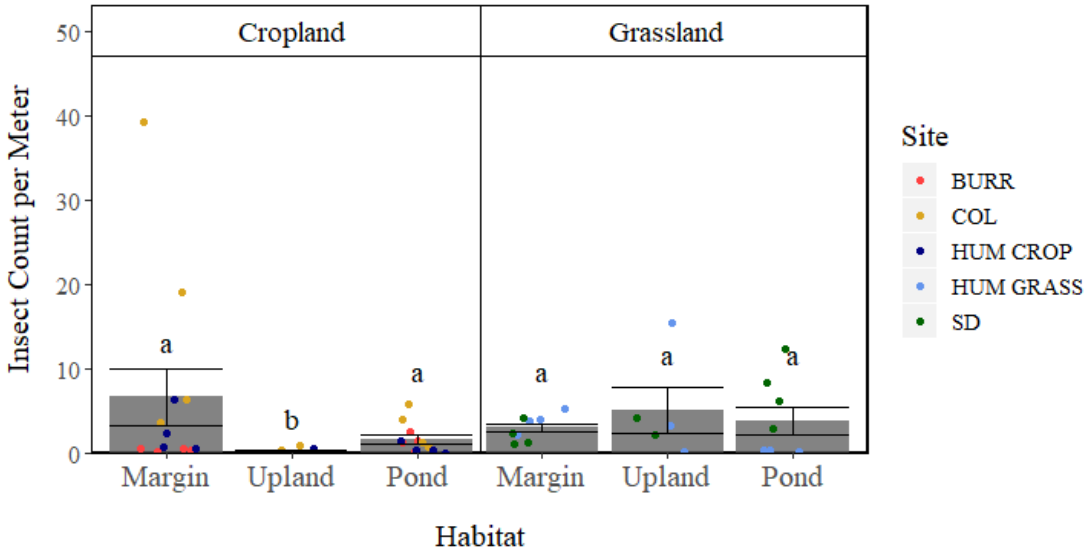

Figure 2.4. Bar chart of arithmetic mean insect count/m by site type (cropland- or grassland-/herbaceous-dominated) and habitat (grassy field "margins," "uplands," or "pond" margins) in 2018. Error bars represent one standard error of the mean. Datapoints are color-coded by site (Col, Colonsay; SD, St. Denis). Significant pairwise comparisons of model-estimated marginal means ($p < 0.05$) are indicated by differing letters.

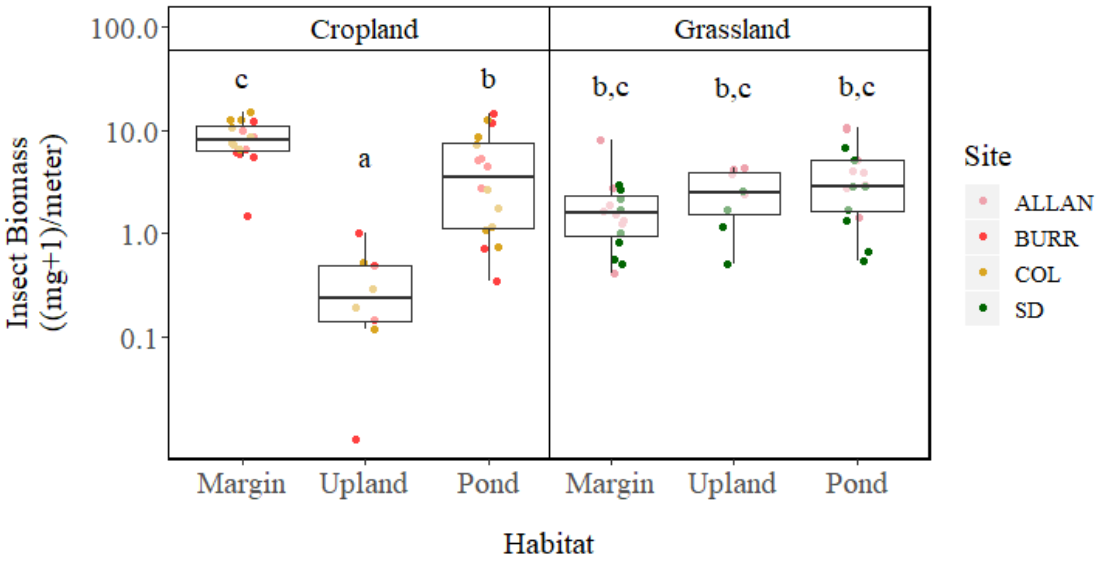

Figure 2.5. Tukey box plot of sweep-net insect biomass ((mg+1)/meter, $\log_{10}$ scale) by site type (cropland- or grassland-dominated) and habitat (grassy field "margins," "uplands," or "pond" margins) in 2017. Datapoints are color-coded by site (Col, Colonsay; SD, St. Denis). Significant pairwise comparisons of model-estimated marginal means ($p < 0.05$) are indicated by differing letters.

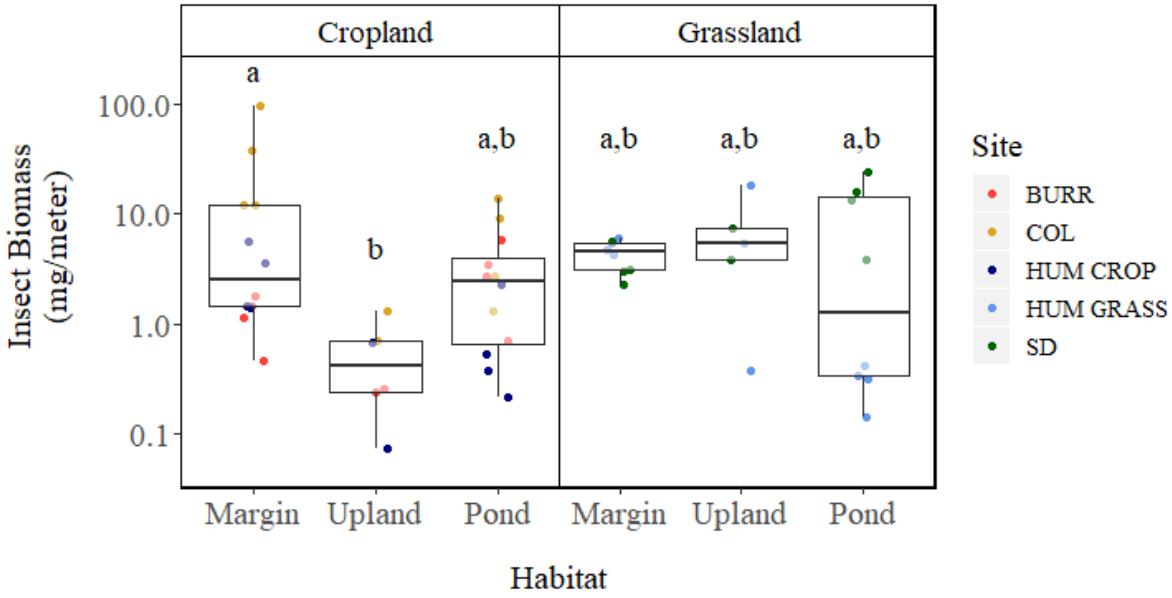

Figure 2.6. Tukey box plot of sweep-net insect biomass (mg/meter, $\log_{10}$ scale) by site type (cropland- or grassland-/herbaceous-dominated) and habitat (grassy field "margins," "uplands," or "pond" margins) in 2018. Datapoints are color-coded by site (Col, Colonsay; SD, St. Denis). Significant pairwise comparisons of model-estimated marginal means ($p < 0.05$) are indicated by differing letters.

PREFACE TO CHAPTER 3

Recent experimental and observational work has suggested the importance of insect prey quality (energy and/or macro-/micro-nutrient composition) to aerial insectivores. Several studies have suggested that aquatic insects and associated nutritional subsidies such as omega-3 long-chain polyunsaturated fatty acids are beneficial to breeding Tree Swallows. There are few published assessments of the nutritional status of swallows or other aerial insectivores in a field setting. The objectives of this chapter were to 1) characterize differences in diet quality (aquatic subsidies of omega-3 long-chain polyunsaturated fatty acids and exposure to neonicotinoid insecticides) for Tree Swallows nesting in prairie agroecosystems and 2) test for positive and negative impacts on nestling swallow growth in relation to omega-3 long-chain polyunsaturated fatty acid status and neonicotinoid exposure. Dr. Chunyan Hao contributed to plasma analysis of neonicotinoids and Dr. Paul Jones contributed to analyses of fatty acids in insects and swallow erythrocyte samples.

CHAPTER 3: CONTRASTING NESTLING DIET QUALITY IN AGROECOSYSTEMS: FATTY ACID STATUS AND EXPOSURE TO NEONICOTINOID INSECTICIDES

3.1 ABSTRACT

Emergent aquatic insects are an energy and nutrient source for Tree Swallows (*Tachycineta bicolor*) which exposes swallows to contaminants sourced from aquatic ecosystems, though terrestrial insects can also act as a source of contaminants in swallow diets. I investigated the potential for aquatic insects to serve as a source of omega-3 long-chain polyunsaturated fatty acids (LC-PUFA) for Tree Swallows nesting in prairie agroecosystems. I also examined exposure to neonicotinoid insecticides. I confirmed that emergent aquatic insects could serve as an important source for omega-3 LC-PUFA eicospentaenoic acid in swallow diets. I found that nestling Tree Swallow fatty acid status differed among study sites, consistent with apparent differences across sites in sampled biomass of emergent aquatic insects. All swallows were also exposed to neonicotinoid insecticides, primarily imidacloprid, but also clothianidin and one detection of thiamethoxam. While nestling swallow exposure to neonicotinoid compounds appeared to differ among sites, imidacloprid exposure in nestlings was not consistently related to the prevalence of local cropping. Nestlings on a grassland-dominated site tended to have lower plasma concentrations of clothianidin than nestlings at sites characterized by cropping near nests. Finally, swallow omega-3 LC-PUFA status was associated with an increase in nestling mass, while association between plasma neonicotinoids and nestling mass was not detected. These results illustrate the importance of aquatic ecosystems, such as prairie ponds, to providing an energy and/or nutrient resource to Tree Swallows, though insectivorous birds may also be exposed to agricultural pesticides consequent to foraging in cropland-dominated landscapes.

3.2 INTRODUCTION

Aquatic and terrestrial food webs are linked by transfers of nutrients and energy; such transfers across habitat boundaries, known as spatial subsidies, can contribute substantially to energy intake among aquatic and terrestrial organisms (Nakano and Murakami 2001, Polis et al. 2002, Schindler and Smits 2017). The export of energy and nutrients from aquatic prey to terrestrial predators is well-documented, and perhaps the most widely studied example is that of emergent aquatic insects (Schindler and Smits 2017). Emergent aquatic insects accumulate nutrients and energy during aquatic juvenile stages and export these resources to terrestrial habitats and consumers on emergence as winged adults (Nakano and Murakami 2001, Krell et al.

2015, Schindler and Smits 2017). Among birds consuming emergent aquatic insect prey are swallows, including Tree Swallows (*Tachycineta bicolor*), with most of the diet of adult and nestling Tree Swallows consisting of aquatic insects, where available (Winkler et al. 2011).

According to North American Breeding Bird Survey (BBS) data, many aerial insectivores, including Tree Swallows, have experienced population declines in parts of their geographic ranges (Sauer et al. 2017, Smith et al. 2015, Michel et al. 2016, Nebel et al. 2010). Aerial insectivores' common reliance on insect prey has suggested a hypothesis that population trends are related to changes in insects (Nebel et al. 2010); still, the evidence that total insect abundance contributes to reproductive success and/or survival of aerial insectivores is ambiguous (Quinney et al. 1986, McCarty and Winkler 1999a, Imlay et al. 2017, McClenaghan et al. 2019a). Recent work suggests that changes in diet quality or composition – as may result from changes in the composition of insect assemblages – may be an important driver of aerial insectivore reproductive success and/or survival (Nocera et al. 2012, Pomfret et al. 2015, Twining et al. 2016b, 2018, English et al. 2018).

Consistent with observations in other regions, Tree Swallows breeding in the Prairie Pothole Region (PPR) of North America tend to consume primarily aquatic insects where available (Michelson et al. 2018). In the PPR, aquatic insects in swallow diets can be derived from prairie ponds (Winkler et al. 2011, Wrubleski and Ross 2011, Michelson et al. 2018). Consequently, agricultural impacts on ponds, especially loss or consolidation via drainage, can impact aquatic insect populations (Wrubleski and Ross 2011), and thereby reduce the availability of aquatic nutritional subsidies to terrestrial predators, such as swallows. While Tree Swallows tend to consume primarily aquatic insects when available, they exhibit dietary flexibility and will consume terrestrial insect taxa (Quinney and Ankney 1985, Johnson and Lombardo 2000, Mengelkoch et al. 2004, Michelson et al. 2018). Therefore, in the absence of aquatic habitats (and consequently, emergent aquatic insects), adult swallows may exhibit a dietary "switch" to consuming and provisioning their nestlings with terrestrial insects (e.g., Johnson and Lombardo 2000).

Twining et al. (2016) reported that supplementation of nestling Tree Swallow diets with omega-3 long-chain polyunsaturated fatty acids (LC-PUFA) enhanced nestling growth and immunocompetence relative to nestlings supplemented only with the precursor α-linolenic acid

(ALA), and inclusion of omega-3 LC-PUFA in diets appeared to be more important than total dietary quantities fed to nestlings. The omega-3 and omega-6 polyunsaturated fatty acids (PUFA) are essential nutrients for all vertebrates studied, including birds, as they are required for normal development and cellular function but cannot be synthesized de novo. Generally, vertebrates can synthesize the more physiologically active omega-3 or omega-6 LC-PUFA (eicosapentaenoic and docosahexaenoic acids, EPA and DHA or arachidonic acid, ARA, respectively) from "short-chain" PUFA precursors (ALA or linoleic acid (LA), respectively), though some carnivorous species appear to have lost this ability (Simopoulos 1991, Sargent et al. 1995) (See Figure 3.1 for a simplified diagram of "short chain" precursor to LC-PUFA conversion). Even in those species capable of this conversion, dietary LC-PUFA appears beneficial, as conversion efficiency tends to be limited (Sargent et al. 1995).

Omega-3 LC-PUFA are produced in abundance by certain aquatic primary producers such as diatoms, cryptophytes, and dinophytes, but not terrestrial plants; as a consequence, there is a decline in concentration of omega-3 LC-PUFA in animal tissues with a dietary shift from aquatic to terrestrial components (Brett and Müller-Navarra 1997, Gladyshev et al. 2009, 2013, Hixson et al. 2015). Consistent with other animals, aquatic insects tend to contain omega-3 LC-PUFA, especially EPA, while terrestrial insects tend to contain lower quantities of these fatty acids (Ghioni et al. 1996, Makhutova et al. 2011, Gladyshev et al. 2013, Hixson et al. 2015, Martin-Creuzburg et al. 2017, Twining et al. 2017, 2019). Terrestrial insects, while generally low in omega-3 LC-PUFA, do contain omega-6 LC-PUFA, perhaps especially ARA (Stanley-Samuelson et al. 1988, Fontaneto et al. 2011, Hixson et al. 2016). While there are several estimates of aquatic insect export of LC-PUFAs to terrestrial ecosystems (Gladyshev et al. 2009, Martin-Creuzburg et al. 2017, Popova et al. 2017), few have directly assessed the importance of aquatic insects as an LC-PUFA subsidy in terrestrial food webs (Schindler and Smits 2017, but see Fritz et al. 2017, Twining et al. 2019).

Twining et al. (2017) further investigated the efficiency with which nestling Tree Swallows convert ALA to omega-3 LC-PUFA DHA and EPA. Twining et al. (2017) estimated that Tree Swallows might derive more total DHA from ALA in moths and butterflies (Lepidoptera) or bees (Hymenoptera: Apidae) than from other taxa, but more total EPA could be derived from aquatic insects. However, the former conclusion requires validation, as Twining et

al. (2017) were unable to determine whether DHA was derived from the EPA present in aquatic insects (cf. Figure 3.1); likewise, these terrestrial taxa are uncommon in swallow diets (Winkler et al. 2011). Growth and mass of offspring have been positively associated with survival and/or recruitment into breeding populations for many passerines, including Tree Swallows (e.g., Shutler et al. 2006). The findings of Twining et al. (2016b) suggest that Tree Swallow nestling intake of aquatic insects, presumably related to omega-3 LC-PUFA intake, could improve nestling condition and ultimately enhance recruitment into breeding populations. Indeed, Twining et al. (2018) reported that aquatic insect biomass, though not terrestrial or total insect biomass, had strong, positive effects on Tree Swallow fledging success.

While emergent aquatic insects provide energy and nutrient subsidies to terrestrial food webs, much recent work has also focused on the potential for aquatic insects to export contaminants from aquatic to terrestrial environments (Sullivan and Rodewald 2012). Export or trophic transfer of numerous contaminants, including mercury, polychlorinated biphenyls (PCBs), and trace metals from emergent aquatic insects to Tree Swallows is well-documented (McCarty 2001, Echols et al. 2004, Smits et al. 2005, Maul et al. 2006, Papp et al. 2007, Brasso and Cristol 2008); however, terrestrial insect prey may also contribute different contaminants to swallow diets (e.g., Smits et al. 2005).

Potential for contamination of prairie ponds with various, primarily agricultural, pesticides is well-established (Donald et al. 1999, 2005, Friesen-Pankratz 2004, Main et al. 2014). Among the most well-studied, recent agrochemical contaminants of prairie ponds are the neonicotinoids, a class of systemic insecticides often used as seed treatments for crops grown in the Prairies (Main et al. 2014, 2015). Neonicotinoids are presumably also widespread in prairie soils, though I am not aware of formal assessments of neonicotinoid soil concentrations, generally (but see Main et al. 2016). Considering there is no mechanism for juvenile stages of soil-dwelling or aquatic insects to avoid exposure from the surrounding medium, this may make them, among non-target species, especially prone to exposure to neonicotinoids and other pesticides (Pisa et al. 2014). Notwithstanding limited bioaccumulation potential (Tomizawa and Casida 2005), neonicotinoids accumulate to some degree in insect tissues (e.g., Camp and Buchwalter 2016). Indeed, neonicotinoids and other agricultural pesticides have previously been detected in Tree

Swallow food boluses (Haroune et al. 2015), suggesting the possible transfer of these insecticides to insectivorous birds.

I investigated the potential for aquatic insects, sourced from prairie ponds, to provide an omega-3 LC-PUFA subsidy to nestling Tree Swallows in prairie agroecosystems. Given widespread presence of neonicotinoids in prairie ponds (Main et al. 2014) and presence in some Tree Swallow diets (Haroune et al. 2015), I also more directly examined swallow exposure to neonicotinoid insecticides via analysis of blood plasma. Finally, I examined whether nestling mass was related to omega-3 LC-PUFA status or neonicotinoid exposure, as a preliminary indicator of positive and negative impacts of nutrient and contaminant intake.

3.3 METHODS

3.3.1 Study Sites

In 2018, I monitored nest boxes at four swallow colonies in southcentral Saskatchewan. Sites were characterized by different land use practices – grazed and un-grazed grassland (1 grassland site, “St. Denis”), crop cultivation (2 cropland sites, “Burr” and “Colonsay”), or crop cultivation alongside uplands seeded to un-grazed herbaceous cover (1 mixed site, “Humboldt”). Allan (a grazed grassland site) was utilized for insect sampling in 2017, but this colony was not studied in 2018 due to high nest failure unrelated to the study.

3.3.2 Tree Swallow Nest Monitoring

Beginning in May 2018, nest boxes were checked for occupancy and egg-laying every 2-3 days. Near the end of the incubation period, nests with complete clutches were checked daily for hatching. The date when the first nestling was observed was assigned as the hatch date (day zero). The number of nestlings hatched was considered the brood size where possible; otherwise, brood size was considered to be the number of nestlings next observed.

3.3.3 Sample Collection and Processing

On day 12 post-hatching, we collected blood samples from two nestlings (pseudo-randomly selected, excluding runts) in 12 broods on each study site (n = 48 broods). Blood samples were collected by venipuncture of the basilic (“wing”) vein using a 27- or 28-gauge needle. Blood samples were collected in heparinized tubes and pooled by nest in a single microcentrifuge tube, which was stored on ice in the field. At this time, nestlings were banded

and measured. Mass was obtained to the nearest 0.25g using a Pesola spring-scale. Head-bill length was measured to the nearest 0.01 mm with dial calipers. Unflattened right wing chord and right ninth primary lengths were measured to the nearest 0.5 mm using a wing rule.

Blood samples were later centrifuged (on day of collection) for 10 min. at 1000 RCF to separate plasma and cells (primarily red blood cells – erythrocytes). Plasma was isolated and stored at -80°C. Erythrocytes were twice rinsed with 200 µL phosphate-buffered saline and centrifuged for five min. at 1000 RCF. Then, 2 µL butylated hydroxytoluene (BHT) in methanol (500 mg/L) was added to erythrocyte samples as an antioxidant, and samples were stored at -80°C. Plasma samples from adult swallows were also obtained as part of another study and were treated in the same manner as nestling plasma samples.

On each study site, 1 liter water samples were also collected from 4 to 5 select ponds utilized for another study during the last two weeks of June 2018. The number of detections and maximum concentrations are reported as a general indicator of the presence of these compounds in ponds across sites. However, these values should not be considered an indicator for each site given limited sampling and high variation in concentrations and detections of these compounds across ponds.

3.3.4 Insect Taxonomic Sorting and Biomass Data

To assess possible contribution of different insect taxa to the fatty acid status of swallows, I utilized samples of insects from systematic sweep-net transects conducted in 2017 as part of another study (see Chapter 2). Though insect fatty acid data are derived from a different sampling year than swallow data, I consider it unlikely that patterns of interest in LC-PUFA (relative comparisons across taxa) would exhibit substantial year-to-year variation. Insect samples were stored at -20°C. Because LC-PUFA are particularly susceptible to autoxidation, even at -20°C (Metherel and Stark 2016, Rudy et al. 2016, Brenna et al. 2018), these data are intended to represent only relative fatty acid composition of insect taxa. Samples were also temporarily thawed and identified to order according to Triplehorn and Johnson (2005). Diptera and Odonata were further sorted to suborder. Nematoceran Diptera were considered to be primarily aquatic in origin, while Brachyceran Diptera were considered to represent a mixture of primarily terrestrial and some aquatic taxa. Other identified taxa were considered primarily terrestrial. Dragonflies, thrips (Thysanoptera, all $\lesssim$1mm), wingless individuals (including

nymphs and larvae), and non-insect taxa were excluded, as these are typically minor components of or absent from swallow diets (Winkler et al. 2011). Prior to fatty acids analysis, samples were pooled by taxon and site; certain taxa were pooled across sites as necessary based on sample availability. Pooled Trichopteran samples were derived from the Allan, Colonsay, and Humboldt sites. Hemiptera were pooled across all sites, with Humboldt more heavily represented by biomass. Lepidoptera were pooled across all sites, with Burr more heavily represented by biomass.

Total biomass for sorted taxa in 2018 is presented as an indicator of the insect prey assemblage on each study site; the same biomass data were previously analyzed in a different context (see Chapter 2). Biomass data were derived from sweep-net transects in different habitat types (cropland or uplands characterized by non-crop vegetation, field margins, or pond margins), but sampling effort was the same across sites. Transects were conducted during the period of peak nestling hatching (9-14 June 2018). I assume sweep-net sampled insect biomass is a proxy of availability of insects on these study sites during the nestling period. The Humboldt site was characterized by both herbaceous cover and cropland in the vicinity of nest boxes and was therefore treated as two sub-sites – referred to as "Humboldt Grass" and "Humboldt Crop," respectively.

3.3.5 Analytical Methods

3.3.5.1 Fatty Acid Extraction and Analyses

Fatty acids in erythrocyte and insect samples were transmethylated and extracted by a modified one-step method of Garcés and Mancha (1993), described below. Erythrocytes reflect long-term dietary fatty acid intake (for nestlings, presumably an aggregated measure over days of life) while plasma reflects recent intake (hours to days)(Arab 2003, Heinze et al. 2012).

When possible based on sample availability, fatty acids were transmethylated and extracted from pooled insect samples in duplicate or triplicate. Pooled insect samples were homogenized using a mortar and pestle, and sample was transferred to tubes prior to reagent addition. A target mass of 50.0 mg was utilized; four samples were <50 mg (28.6 to 41.1 mg). Prior to fatty acid extraction, 100 µL reverse osmosis water was added to ~50 µL thawed erythrocyte samples, mixed, and 100 µL was transferred to tubes for fatty acid extraction.

Fatty acids were transmethylated and extracted from insect and erythrocyte samples using 15mL Kimble KIMAX conical-bottom glass centrifuge tubes (DWK Life Sciences, No. K7378515) lined with PTFE thread seal tape to prevent reagent evaporation, with phenolic PTFE-faced caps (DWK Life Sciences, No. K7380215415). 1.45 mL n-Heptane containing 100 mg/L BHT and 3.55 mL of reagent mixture (methanol:toluene:2,2-dimethoxypropane:H_2SO_4, 39:20:10:2 by volume) were transferred to tubes. Tubes were capped, sample and reagent mixed, and transferred to a heated water bath at 80°C. After five minutes heating, tubes were removed, mixed to form a single phase, and returned to the heated water bath. After 2 hours heating, tubes were removed and thoroughly mixed again. To improve phase separation, 2 mL saturated NaCl solution was added and mixed, and tubes were centrifuged at 500 RCF for 5 minutes. The upper organic layer containing fatty acid methyl esters (FAMEs) was then transferred to GC vials and stored at -80°C.

FAMEs were identified using GC-MS. Because substantial information on conversion efficiencies and deposition of fatty acids among tissues is required, the use of fatty acids as a quantitative dietary tracer in swallows is not currently possible (and see Jardine et al. 2015, Twining et al. 2016a). Therefore, I used the ratio of eicosapentaenoic acid (an omega-3 LC-PUFA) to arachidonic acid (an omega-6 LC-PUFA) chromatogram peak area as a proxy for omega-3 LC-PUFA composition and contribution of aquatic and terrestrial components to insect and swallow diets. Chromatogram peaks for EPA and ARA FAMEs were identified for an external standard (Supelco 37-component FAME mix, CRM47885, Sigma-Aldrich) using Thermo Scientific Xcalibur version 4.1.31.9 (Thermo Fisher Scientific, Inc.) in tandem with NIST MS Search (National Institute of Standards and Technology Mass Spectral Search Program and Library System). EPA and ARA peaks were identified in samples by comparison of retention times to identified standard peaks, and peak areas were determined. Samples were dropped if EPA or ARA peaks had a signal-to-noise ratio <1 (n = 3 nestling samples) or if either peak was not detected.

3.3.5.2 Neonicotinoid Analyses

Nestling plasma pools (20 to 50 µL, n = 43 nestling, n = 13 adult) were screened for neonicotinoids (acetamiprid, clothianidin, imidacloprid, nitenpyram, thiacloprid, and thiamethoxam, as well as flonicamid and neonicotinoid metabolite 6-chloronicotinic acid (6-

CNA)) using an LC-MS/MS method described by Hao et al. (2018). Volumes of plasma were 50, 40, 25, or 20 µL. Method detection limits (MDLs) were as follows: 6-CNA, 177.7 ng/L; acetamiprid, 3.6 ng/L; clothianidin, 7.4 ng/L; flonicamid, 15.9 ng/L; imidacloprid, 4.6 ng/L; nitenpyram, 8.8 ng/L; thiacloprid, 2.3 ng/L; thiamethoxam, 4.5 ng/L. All compounds, excepting thiamethoxam, were <MDL in plasma blanks (n = 4) derived from captive European Starlings (*Sturnus vulgaris*) plasma pools; thiamethoxam was present in these samples at an average concentration of 370.7 ng/L, presumably derived from a commercial seed mix diet. Average recoveries of spiked samples (n = 8) were as follows: 6-CNA, 101.0%; acetamiprid, 106.5%; clothianidin, 110.5%; flonicamid, 93.2%; imidacloprid, 114.3%; nitenpyram, 79.3%; thiacloprid, 99.8%; thiamethoxam, 110.6%. Values were not recovery corrected.

Pond water samples were screened for certain neonicotinoid parent compounds (acetamiprid, clothianidin, imidacloprid, and thiamethoxam, as well as flonicamid) using a solid-phase extraction and LC-MS/MS method described by Main et al. (2014). Mean limits of detection (LODs, n = 10) were as follows: acetamiprid, 0.0003 µg/L; clothianidin, 0.0011 µg/L; imidacloprid, 0.0010 µg/L; thiamethoxam, 0.0025 µg/L; flonicamid, 0.0007 µg/L. Mean limits of quantification (LOQs, n = 10) were as follows: acetamiprid, 0.0009 µg/L; clothianidin, 0.0034 µg/L; imidacloprid, 0.0031 µg/L; thiamethoxam, 0.0074 µg/L; flonicamid, 0.0022 µg/L. Mean quality control (n = 10) recoveries ± relative standard deviation were as follows: acetamiprid, 116.2% ± 10.4; clothianidin, 63.5% ± 14.9; imidacloprid, 98.3% ± 17.1; thiamethoxam, 93.6% ± 21.5; flonicamid, 54.0% ± 13.6. These compounds were not detected in laboratory blanks (n = 10). Values were recovery corrected.

3.3.6 Data Analyses

Statistical analyses and generation of figures were conducted in R (version 3.6.0) (R Core Team 2018). Insect EPA:ARA peak area ratios were calculated for each site and taxon pool. EPA:ARA peak area ratios were also calculated for each nestling erythrocyte pool. To test for site differences in EPA:ARA peak area ratios for nestling erythrocyte samples, I used a one-way analysis of variance (ANOVA) approach. EPA:ARA peak area ratios were log-transformed to improve normality of residuals. I used package emmeans (Lenth 2018) for pairwise comparisons, by site, of model-estimated means using Tukey-adjusted p-values.

I tested for a correlation between log-transformed plasma concentrations of imidacloprid and clothianidin, using concentrations from both adult and nestling plasma, using Pearson's product-moment correlation coefficient and a two-sided t-test; due to a substantial degree of censoring (values less than the method detection limit) for clothianidin, I utilized only those values from swallows with detections of clothianidin.

To test for site differences in nestling plasma concentrations of imidacloprid, I fit a linear model using generalized least squares (GLS) with the "gls" function of package nlme (Pinheiro et al. 2019). Plasma concentrations were log-transformed to improve normality of residuals, and the "varIdent" variance structure was used to account for heterogenous residual variance by site. A Wald Chi-square test was conducted to assess statistical significance.

To test for site differences in nestling plasma concentrations of clothianidin, including censored data <MDL, I used package NADA (Lee 2017) and package survival (Therneau and Grambsch 2000, Therneau 2015) to fit a parametric survival regression model with a log-normal distribution. The MDL value was substituted for values <MDL, which were also modelled as left-censored values. A likelihood-ratio test was conducted to assess statistical significance. One outlier (high value from the Humboldt site) was dropped to improve normality of residuals; inclusion or exclusion of this value had no impact on statistical significance ($\alpha = 0.05$). For both models, package emmeans (Lenth 2018) was used for pairwise comparisons, by site, of model-estimated means using Tukey-adjusted p-values. Due to sample size for adults, site and age (adult or nestling) were confounded. Therefore, data from adult swallows was not incorporated in any models, but these data are included in summary statistics.

I fit linear mixed-effects models via package lme4 (Bates et al. 2015) to nestling body mass as measured on day 12 of life (n = 43 broods, 260 nestlings), incorporating fixed effects of head-bill length, EPA:ARA ratio, plasma neonicotinoid concentration, and brood size and a random-intercept term for brood identity (nest box). Head-bill length was incorporated as a fixed effect to control for structural size, and hence models reflect mass corrected for head-bill length – a potential proxy for condition (energy reserves). Head-bill length was more strongly correlated to nestling mass than other length measures; however, which length measures, if any, can be utilized in such analyses requires empirical verification in swallows. The total plasma neonicotinoid concentration was calculated assuming that <MDL values were zeros, as I

considered it reasonable that some swallows do not experience substantial exposure to certain compounds. The EPA:ARA ratio or plasma neonicotinoid concentration from sampled nestlings was used as an indicator for all nestlings within a given brood. Because plasma neonicotinoid concentrations were unavailable for some broods, a second model was fit, dropping the plasma neonicotinoid effect to assess the effect of increasing sample size (n = 45 broods, 276 nestlings) on estimates for the EPA:ARA ratio effect. Statistical significance ($\alpha = 0.05$) for the EPA:ARA ratio effect was not altered in this model. One nestling was dropped from analyses due to mass incompatible with the Pesola spring-scale (i.e., impossible measurement). Statistical significance was assessed using Type II Wald F-tests with the Kenward-Roger degrees of freedom approximation via package car (Fox and Weisberg 2019).

The threshold for statistical significance (α) in all analyses was set at 0.05. I used package NADA (Lee 2017) to calculate summary statistics for censored data using regression on order statistics (ROS) with a lognormal distribution. I used package ggplot2 (Wickham 2009) to generate figures and package effects (Fox and Weisberg 2018, 2019) to visualize models.

3.4 RESULTS

3.4.1 EPA:ARA Ratios of Insect Taxa

Nine insect taxa were represented in fatty acid analyses – caddisflies (Trichoptera), damselflies (Anisoptera: Zygoptera), Nematoceran Diptera, Brachyceran Diptera, beetles (Coleoptera), grasshoppers (Orthoptera), true bugs (Hemiptera), sawflies, wasps, bees, and possibly flying ants (Hymenoptera), and moths and butterflies (Lepidoptera). Mean (standard deviation, as applicable) EPA:ARA ratios for each insect taxon across sites were as follows: Trichoptera, 7.4; Zygoptera, 6.5 (0.7); Nematocera, 3.8 (0.9); Brachycera, 2.5 (0.5); Coleoptera, 1.0 (0.6); Orthoptera, 1.0 (0.8); Hemiptera, 3.8; Hymenoptera, 4.6 (2.4) (Figure 3.2, Table B1). Eicosapentaenoic acid, but not arachidonic acid, was detected in Lepidoptera.

3.4.2 Nestling Erythrocyte EPA:ARA Ratios and Aquatic Insect Biomass

One-way ANVOA indicated that nestling fatty acid status (log-transformed EPA:ARA ratios) differed among sites ($F_{3,41} = 51.7$, $p < 0.001$, Figure 3.3, Table B2). Geometric mean (geometric standard deviation) nestling EPA:ARA ratios by study site were as follows: Burr, 0.19 (1.24); Colonsay, 0.55 (1.21); Humboldt, 0.45 (1.18); and St. Denis, 0.40 (1.29). Sampled nestlings at Burr had lower EPA:ARA ratios than nestlings at other sites. Site differences were

reflected in pairwise comparisons of model-estimated means. Nestlings at Burr had lower EPA:ARA ratios than nestlings at Colonsay ($t(41) = -11.63$, $p < 0.001$), Humboldt ($t(41) = -9.67$, $p < 0.001$), and St. Denis ($t(41) = -8.01$, $p < 0.001$). Nestlings at Colonsay tended to have greater EPA:ARA ratios than those at St. Denis ($t(41) = 3.6$, $p = 0.004$). Pairwise comparisons between Colonsay and Humboldt ($t(41) = 2.21$, $p = 0.14$) or Humboldt and St. Denis ($t(41) = 1.49$, $p = 0.46$) were not statistically significant. These site differences may track differences in sampled biomass of primarily aquatic taxa (summed biomass of caddisflies, damselflies, and Nematoceran Diptera) on each study site (Figure 3.4, Table 3.1).

3.4.3 Tree Swallow Exposure to Neonicotinoids

Imidacloprid was detected in 100% of adult and nestling swallows sampled (n = 56), with a geometric mean (geometric standard deviation) plasma concentration of 155.0 ng/L (3.2). The minimum plasma concentration of imidacloprid in sampled swallows was 6 ng/L (adult swallow at St. Denis) and the maximum plasma concentration was 1780 ng/L (nestling pool at Burr). Clothianidin was detected in 69.6% of adult and nestling swallows (n = 39/56), with a mean (standard deviation) plasma concentration of 28.9 ng/L (32.0), calculated by regression on order statistics, and a maximum concentration of 198 ng/L (nestling pool at Humboldt). Thiamethoxam was only detected in one nestling swallow plasma pool from the Humboldt site at a concentration of 9.7 ng/L. Other compounds were <MDL in all plasma samples. There was no statistically significant correlation between log-transformed concentrations of imidacloprid and clothianidin values >MDL ($r(37) = 0.09$, $p = 0.59$).

Based on the GLS model, there were statistically significant differences in nestling plasma concentrations of imidacloprid between sites ($\chi^2(3) = 33.9$, $p < 0.001$, Table B3, Figure 3.5). Geometric mean (geometric standard deviation) nestling plasma concentrations of imidacloprid by study site were as follows: Burr, 272.9 ng/L (2.2); Colonsay, 113.2 ng/L (2.3); Humboldt, 479.5 ng/L (1.6); St. Denis 89.3 ng/L (4.0). Pairwise comparisons of model-estimated means were statistically significant between Humboldt and Colonsay ($t(15.1) = 4.95$, $p = 0.001$) or Humboldt and St. Denis ($t(12.3) = 3.79$, $p = 0.01$). Other pairwise comparisons were not statistically significant: Colonsay and Burr ($t(19.9) = -2.5$, $p = 0.09$); St. Denis and Burr ($t(15.8) = -2.3$, $p = 0.14$); St. Denis and Colonsay ($t(16.4) = -0.48$, $p = 0.96$); Humboldt and Burr ($t(15.6) = 2.01$, $p = 0.23$).

Based on the parametric survival model, nestling plasma clothianidin concentrations differed between sites where nestlings hatched (χ^2 (3) = 36.21, p < 0.001, Table B4, Figure 3.5). Clothianidin was >MDL in only 2 of 11 nestling plasma samples from St. Denis but was detected in all nestling plasma samples (n = 32) from other study sites with cultivated cropland near all nest boxes (<100 m). Geometric mean (geometric standard deviation) nestling plasma concentrations of clothianidin, for sites characterized by cultivated cropland near nests, were as follows: Burr, 21.5 ng/L (1.8); Colonsay, 43.2 ng/L (1.8); Humboldt, 36.8 ng/L (2.1). Pairwise comparisons of model-estimated means were statistically significant between Burr and St. Denis (t(37) = 4.02, p = 0.002), Colonsay and St. Denis (t(37) = 6.15, p < 0.001), or Humboldt and St. Denis (t(37) = 4.89, p < 0.001). Other pairwise comparisons were not statistically significant: Burr and Colonsay (t(37) = -2.51, p = 0.07); Burr and Humboldt (t(37) = -1.19, p = 0.63); Colonsay and Humboldt (t(37) = 1.19, p = 0.64).

Pond water sampling consistently confirmed the presence of imidacloprid and clothianidin in ponds across sites with cropping present near nest boxes (Table 3.2). Clothianidin was detected at lower maximum concentrations than imidacloprid within a given site. Thiamethoxam was detected only at Burr and Humboldt and at lower maximum concentrations than imidacloprid or clothianidin within a given site. Acetamiprid was not detected in any pond water samples, while flonicamid was detected in only one water sample at the Colonsay site at a concentration <LOQ. Neonicotinoids and flonicamid were not detected in pond water samples at St. Denis.

3.4.4 Predictors of Nestling Mass

From the model of nestling mass, the effect of EPA:ARA ratio was statistically significant, though weakly supported ($F_{1,39.0}$ = 4.5, p = 0.04, Table B5, B6). Model results suggested a positive association between EPA:ARA ratios and nestling mass (Figure 3.7). Effect of brood size or neonicotinoid concentrations were not statistically significant.

3.5 DISCUSSION

3.5.1 Insect Sources of Fatty Acids

I confirmed that different insect taxa differed in LC-PUFA composition, as reflected by EPA:ARA ratios. Primarily aquatic Trichoptera, damselflies, and Nematoceran Diptera tended to have greater EPA:ARA ratios than primarily terrestrial Brachyceran Diptera, Coleoptera, and

Orthoptera. These results are generally consistent with previous findings suggesting omega-3:omega-6 ratios of animal tissues, including insects, can be used as an index to the contribution of aquatic and terrestrial components of diet (Torres-Ruiz et al. 2007, Hixson et al. 2015). However, Hymenoptera and Hemiptera had EPA:ARA ratios similar to those of aquatic taxa, and in Lepidoptera, EPA, but not ARA, was detected. It is unclear whether these patterns are indicative of an aquatic juvenile stage in these taxa. Some aquatic Hymenoptera and Hemiptera are present on our study sites (Elgin, pers. obs.); however, these higher ratios may simply be a consequence of low concentrations of LC-PUFA, or indeed lower total lipid content (Hanson et al. 1985). Some EPA:ARA ratios assessed here are consistent with presumed insect diet, as associated with habitat and trophic level (Hanson et al. 1985, Torres-Ruiz et al. 2010, Hixson et al. 2015). For example, almost exclusively terrestrial beetles have substantially lower EPA:ARA ratios than aquatic damselflies. Damselfly naiads are predatory, while larvae of Nematoceran Diptera (here, primarily Culicomorpha) occupy multiple trophic levels, with many detritivorous species. Despite that both these taxa are presumably associated with aquatic habitats, "average" trophic level is presumably reflected by higher EPA:ARA ratios among damselflies than Nematoceran Diptera. Importantly, these data suggest that Tree Swallows' differential consumption of these insect taxa has potential to alter swallow EPA:ARA ratios.

3.5.2 Nestling Omega-3 LC-PUFA Status in Relation to Aquatic Insect Availability

The site where nestlings hatched appeared to have a strong relationship with nestling EPA:ARA ratios; namely, at Burr, nestlings had lower EPA:ARA ratios than nestlings sampled at St. Denis, Colonsay, or Humboldt. Low EPA:ARA ratios presumably reflect the loss of ponds due to continuous agricultural drainage on the Burr site (Michelson 2015) and lower presumed availability of aquatic insects as represented by biomass data (Figure 3.4). Nestlings sampled at Colonsay tended to have greater EPA:ARA ratios than those sampled at St. Denis, which also appears to reflect lower biomass of aquatic insects at St. Denis relative to Colonsay. The nature of the Humboldt site complicates interpretation of insect availability, but I suggest overall aquatic insect availability to swallows may indeed be intermediate between that of St. Denis and Colonsay, given that swallows will exploit concentrations of flying or actively emerging insects. The difference between the portions of the Humboldt site characterized by semi-natural cover and cropland are probably attributable to the clustering of small, poor-flying Nematoceran Diptera in denser vegetation (see Chapter 2). It is not clear whether EPA:ARA ratios, or omega-3

LC-PUFA status of blood, generally, is more a more accurate indicator of either total aquatic insect intake or relative proportion of aquatic and terrestrial insects in the diet of swallows. I speculate that the two components are almost inextricably linked for free-living Tree Swallows, given the typical prevalence of aquatic insects in Tree Swallow diets and their dietary flexibility (Winkler et al. 2011). Nevertheless, differences in swallow EPA:ARA ratios on these study sites, with apparent site differences in biomass of aquatic and terrestrial insect prey, are consistent with the hypothesis that prairie ponds act as a source of omega-3 LC-PUFA, transferred by aquatic insects as a nutrient subsidy to nestling swallows.

3.5.3 Tree Swallow Exposure to Neonicotinoid Insecticides

Here, I confirmed exposure to neonicotinoid insecticides in free-living, primarily insectivorous swallows using new methods for sensitive low volume analysis of blood plasma. Consistent with several emerging studies on birds, the detection of neonicotinoids in all swallow plasma samples confirms widespread exposure of wild birds to neonicotinoids (Taliansky-Chamudis et al. 2017, Bishop et al. 2018, Byholm et al. 2018, Ertl et al. 2018, Hao et al. 2018, MacDonald et al. 2018, Graves et al. 2019, Humann-Guilleminot et al. 2019). Compared with the levels reported by Hao et al. (2018) in another passerine species, White-crowned Sparrows (*Zonotrichia leucophrys*) sampled in southern Ontario on migration, swallows sampled in Saskatchewan tended to have higher concentrations and detection frequency of imidacloprid and clothianidin than those sparrows at capture. However, thiacloprid, thiamethoxam, and acetamiprid were also detected infrequently in sparrow blood plasma (Hao et al. 2018). In an assessment of plasma neonicotinoids of nestling Eurasian Eagle-owls (*Bubo bubo*), Taliansky-Chamudis et al. (2017) reported that only imidacloprid was detected in one of thirty plasma samples at a concentration of 3280 ng/L; however, method detection limits were approximately three orders of magnitude greater than the method utilized here (Hao et al. 2018). Additional work is required to assess whether differences between compounds (e.g., clothianidin and imidacloprid) are fully attributable to differential intake or also to metabolic differences, which may explain differential toxicity of neonicotinoid compounds to birds (Addy-Orduna et al. 2019). Still, results here are consistent with the findings of Haroune et al. (2015) – neonicotinoid exposure is not restricted to granivores, herbivores, or higher trophic levels, but also occurs amongst insectivorous passerines.

Swallow exposure to certain neonicotinoids (and other agricultural pesticides) will likely vary from year to year due to multiple factors, including crop rotation and precipitation (e.g., Main et al. 2015). Still, there is some evidence for greater persistence of neonicotinoids in cooler, drier soils such as might be found in Prairie Canada; for example, the soil half-life (DT_{50}) for clothianidin has been reported as 385 days in Ontario, in contrast to 1386 days in North Dakota (PMRA 2004). Neonicotinoids may be persistent in low-light conditions of pond sediments (water hydrolysis DT_{50} > 1 year) (Morrissey et al. 2015), but most current evidence has not demonstrated persistence in pond sediments. Main et al. (2015) reported neonicotinoid detections in only 6% of pond sediment samples in summer 2012, in contrast to 62% of water samples in the same period. Some degree of neonicotinoid persistence in agricultural soils of the Prairies, with subsequent runoff in snowmelt, has been demonstrated (Main et al. 2016).

Contrary to expectation, imidacloprid concentrations in nestling swallow plasma were not associated with local cropping, though concentrations of clothianidin were higher at sites with cultivated cropland near nest boxes. It is possible that differential exposure to imidacloprid relative to clothianidin at St. Denis is, in part, attributable to differential persistence of imidacloprid and past uses of this compound (e.g., Jones et al. 2014). Still, the substantial variability of plasma concentrations on the St. Denis site, relative to other sites, is suggestive of more varied intake of imidacloprid, and imidacloprid was not detected in pond water samples at St. Denis in 2018. Assuming neonicotinoids are sourced from insect prey, it is possible that contaminated insects are dispersing from local cropland, or that swallows are foraging in the vicinity of cropland. I consider it unlikely that any large quantity of imidacloprid was deposited on site due to atmospheric deposition, given that neonicotinoids have low potential for volatilization (Bonmatin et al. 2015), but imidacloprid may be used on site or transferred from nearby cropland via precipitation runoff and/or snowmelt (e.g., Main et al. 2016). Additionally, previous experimental wetland studies have utilized imidacloprid in a pond ("Pond 2") in close proximity to the St. Denis (grassland) swallow colony (Cavallaro et al. 2018, Maloney et al. 2018). Cavallaro (2018) previously reported detectable concentrations (0.01 to 0.10 µg/L) of imidacloprid, but not clothianidin or thiamethoxam, in Pond 2 one year following an addition experiment. Water samples in 2018 also had frequent detections of clothianidin and imidacloprid at other sites, which suggests differences in plasma neonicotinoid concentrations between study sites may be related to local environmental contamination. Future work should aim to further

characterize sources of neonicotinoids in swallow diets as well as the ubiquity and persistence of these compounds in prairie soils and pond sediments.

3.5.4 Nestling Mass in Relation to EPA:ARA Ratio and Plasma Neonicotinoids

I found that an increase in nestling EPA:ARA ratios was associated with an increase in nestling mass, while relationships with plasma neonicotinoid concentrations were not detected. The positive association of nestling mass with EPA:ARA ratios lends support to the hypothesis that prey quality and/or diet composition is an important factor affecting nestling swallow mass and possibly nestling condition (Twining et al. 2016b). Still, these results are entirely correlative. Several other factors might contribute to nestling mass and condition, including quantity of prey delivered to nestlings or other nutrients associated with insect fatty acid composition. Dietary calcium, for example, appears to contribute to Tree Swallow nestling growth (Dawson and Bidwell 2005), and aquatic insects may also act as a calcium subsidy to Tree Swallows. However, provisioning of nestlings with more calcium-rich items (mollusk shells) also occurs on the Burr site (Elgin, pers. obs.). It is also possible that neonicotinoid concentrations from sampled nestlings were not reflective of the entire brood, as modeled. Nestlings on our study sites are also exposed to an array of pesticides detected in food bolus samples (unpubl. data). This suggests potential for confounding, additive, or interactive effects of exposure to multiple contaminants that would remain undetected. Especially given that plasma concentrations of neonicotinoids alone are uncorrelated, plasma neonicotinoid concentrations are unlikely to reflect total contaminant loads in swallows. Though I did not detect any significant effects of neonicotinoid exposure, such exposures raise the question of whether direct effects of neonicotinoid toxicity – such as mass loss demonstrated in several non-insectivorous species (Lopez-Antia et al. 2013, Eng et al. 2017, 2019, Addy-Orduna et al. 2019) – play any role in association between neonicotinoid concentrations and population trends of some insectivorous birds (Hallmann et al. 2014).

3.5.5 Conclusions

I found that nestling swallow fatty acid status differed among study sites – differences which were reflective of aquatic insect biomass on each site. Fatty acid status (EPA:ARA ratio) was associated with an increase in nestling mass, underscoring the importance of aquatic insect prey to breeding Tree Swallows. Still, swallows were also exposed to neonicotinoid insecticides,

which appears to be, in part, a consequence of breeding in landscapes dominated by intensive cropping. These findings emphasize the importance of preserving, restoring, and protecting aquatic habitats like prairie ponds as a conservation measure for swallows breeding in agricultural landscapes. Future work should attempt to disentangle the impacts of prey quantity and quality (beneficial nutrients and deleterious contaminants) on additional aerial insectivorous species.

TABLES AND FIGURES

Table 3.1. Summary table of insect biomass by taxon on each study site or sub-site in 2018. Values represent the sum across sweep-net transects on a given study site. Presumed habitat association of juvenile stages is indicated for each insect taxon. Burr and Colonsay are cropland-dominated, St. Denis is grassland-dominated, and Humboldt is characterized by roughly equal proportions of cropland (Humboldt Crop sub-site) and herbaceous vegetation (Humboldt Grass sub-site) near nest boxes.

	Study Site				
Taxon (Habitat)	Burr	Colonsay	Humboldt Crop	Humboldt Grass	St. Denis
Trichoptera (Aquatic)	0	0	0	0	25.6
Zygoptera (Aquatic)	19.2	172	38.2	52.1	263.8
Nematocera (Aquatic)	64.9	3622.1	302.1	2437.8	1032.1
Brachycera (Terrestrial/Aquatic)	588.2	818.2	90.6	93.5	1500.8
Coleoptera (Terrestrial)	27.3	562.5	15.1	23	887.4
Orthoptera (Terrestrial)	0	48.3	80.5	0	0
Lepidoptera (Terrestrial)	17.2	70.8	0	0	7
Neuroptera (Terrestrial)	0	8.2	0	0	0
Hemiptera (Terrestrial)	34.3	76.2	4.9	29.7	452.6
Hymenoptera (Terrestrial)	52	85.4	13.8	17.2	157.4
Total	803.1	5463.7	545.2	2653.3	4326.7

Table 3.2. Summary of detections and maximum concentrations (ng/L, recovery-corrected) of neonicotinoids and flonicamid in pond water samples near each study site. Burr and Colonsay are cropland-dominated, St. Denis is grassland-dominated, and Humboldt is characterized by roughly equal proportions of cropland and herbaceous vegetation near nest boxes. Sample sizes (n) for each site are indicated. Maximum values <LOQ (based on uncorrected values) are indicated by an asterisk (*). ND, not detected.

Site (no. ponds, n)	Imidacloprid Detects, Max. (ng/L)	Clothianidin Detects, Max. (ng/L)	Thiamethoxam Detects, Max. (ng/L)	Acetamiprid Detects, Max. (ng/L)	Flonicamid Detects, Max. (ng/L)
Burr (4)	3, 477	3, 28	3, 12	0, ND	0, ND
Colonsay (5)	1, 5	2, 4*	0, ND	0, ND	1, 2*
Humboldt (4)	3, 42	3, 13	1, 4*	0, ND	0, ND
St. Denis (5)	0, ND	0, ND	0, ND	0, ND	0, ND

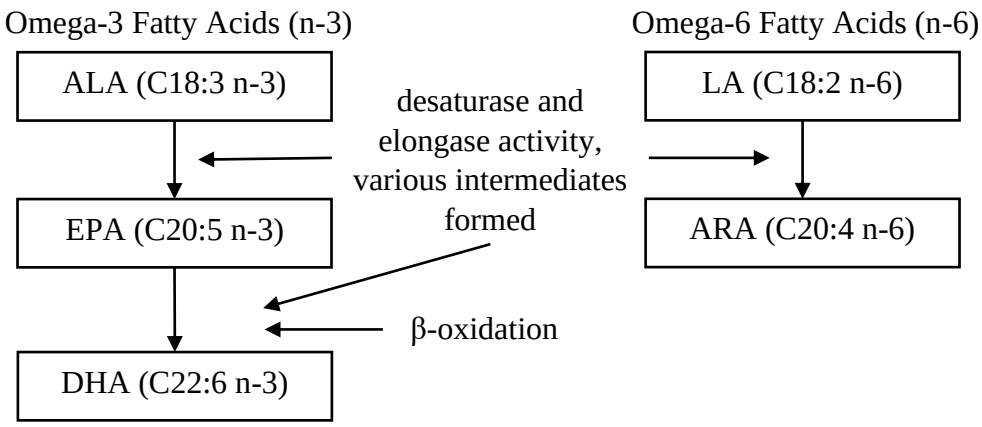

Figure 3.1. Simplified conversion pathway for eicosapentaenoic acid and docosahexaenoic acid (EPA and DHA, respectively) from alpha-linolenic acid (ALA) and arachidonic acid (ARA) from linoleic acid (LA). Modified from Haghighi et al. (2015).

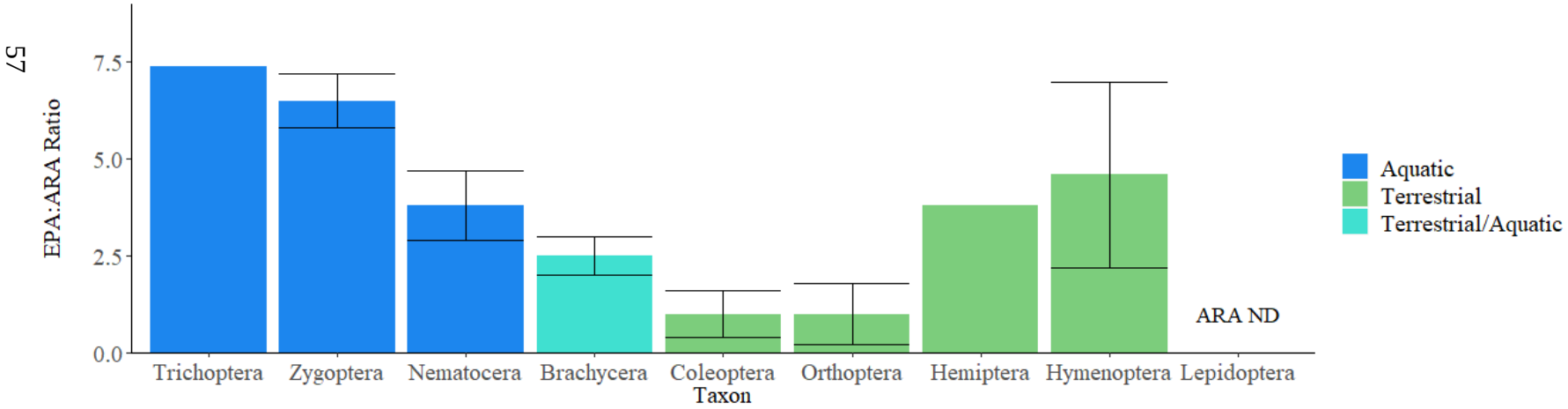

Figure 3.2. Eicosapentaenoic acid: arachidonic acid (EPA:ARA) ratios for insect taxa, derived from 2017 samples. Height of bars indicates mean across sites. Error bars represent standard deviation across sites, where applicable. Presumed habitat association of juvenile stages are color-coded for each taxon (Trichoptera, n = 1, pooled across 3 sites; Zygoptera, n = 5 sites; Nematocera, n = 5 sites; Brachycera, n = 5 sites; Coleoptera, n = 5 sites; Orthoptera, n = 3 sites; Hemiptera, n = 1, pooled across 5 sites; Hymenoptera, n = 3 sites. Arachidonic acid was not detected (ND) in Lepidoptera, n = 1, pooled across 5 sites).

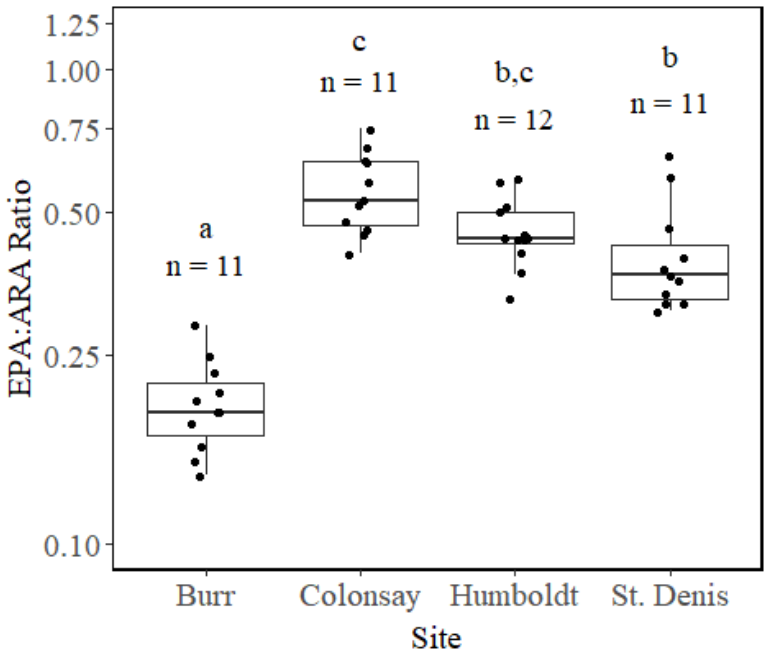

Figure 3.3. EPA:ARA ratios (log_{10} scale) of nestling Tree Swallow erythrocyte samples by study site in 2018. Burr and Colonsay are cropland-dominated. St. Denis is grassland-dominated. Humboldt is characterized by roughly equal proportions of cropland and herbaceous vegetation near nest boxes. Differing letters indicate statistically significant ($p < 0.05$) pairwise comparisons of model-estimated means between sites.

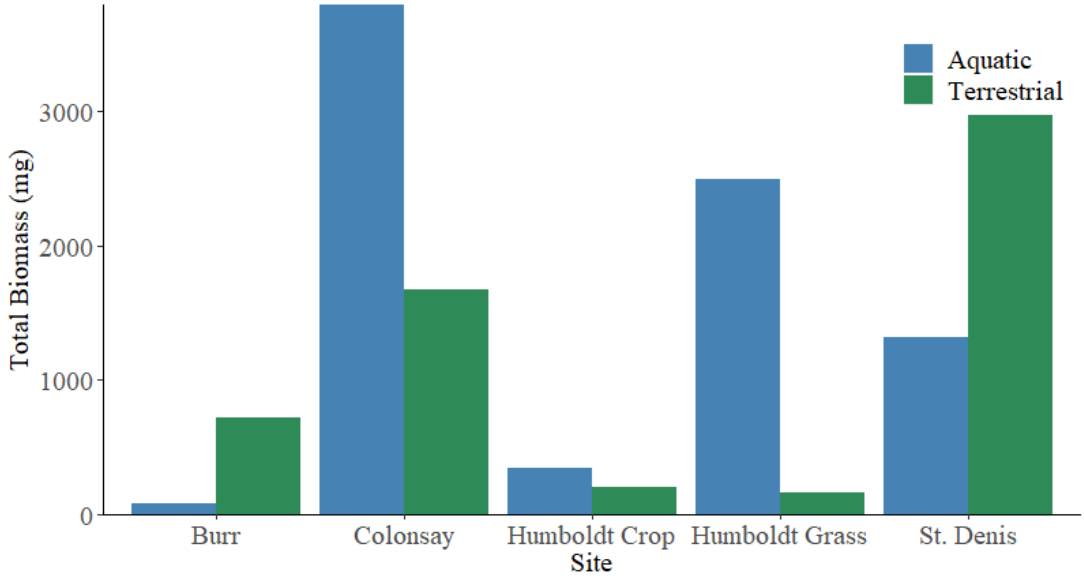

Figure 3.4. Bar chart of aquatic and terrestrial insect biomass (mg) in 2018, by site or sub-site. Height of bars indicates the total biomass across sweep-net sampling transects for taxa considered aquatic or primarily terrestrial, including Brachyceran Diptera. Burr and Colonsay are cropland-dominated. St. Denis is grassland-dominated. Humboldt is characterized by roughly equal proportions of cropland (Humboldt Crop sub-site) and herbaceous vegetation (Humboldt Grass sub-site) near nest boxes.

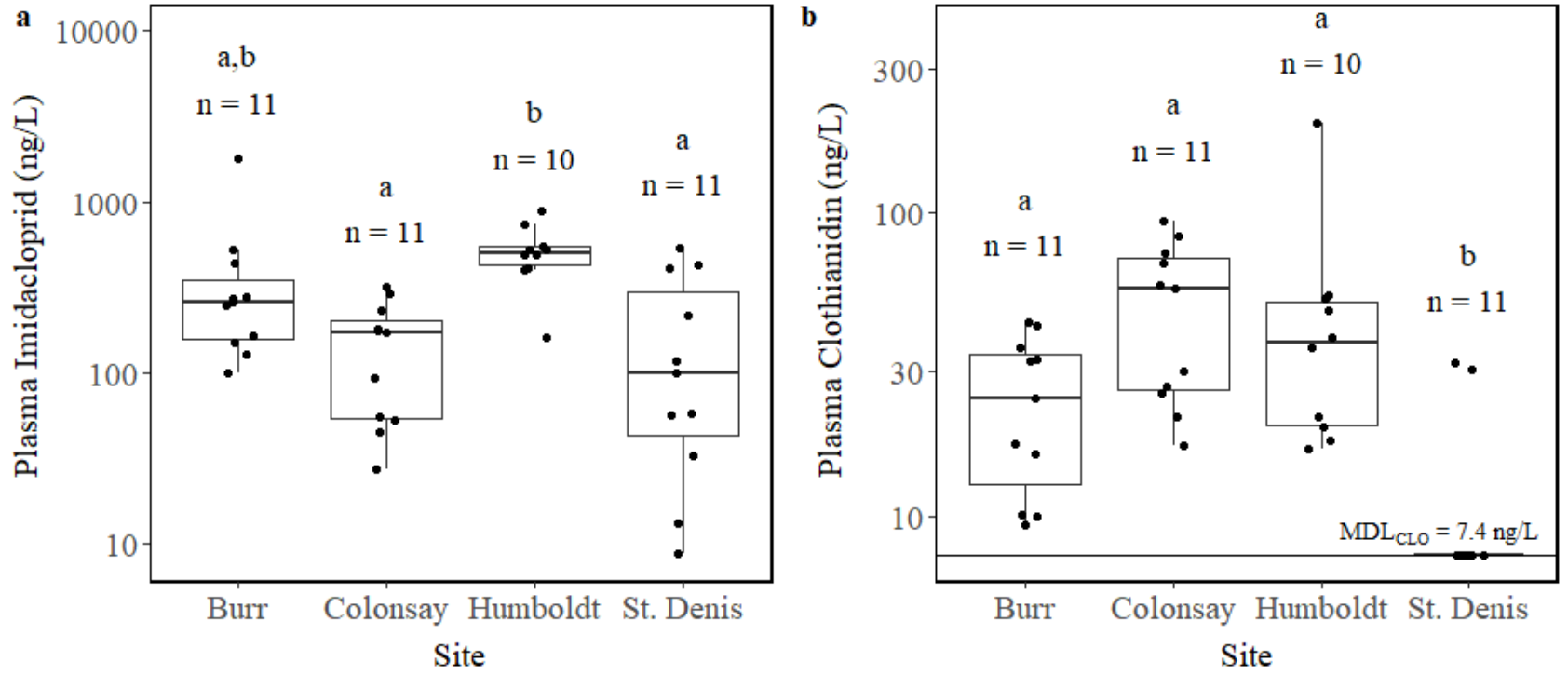

Figure 3.5. Left (a), Tukey boxplot of nestling plasma imidacloprid concentrations (ng/L, $\log_{10}$ scale) on each study site. Right (b), Tukey boxplot of nestling plasma clothianidin concentrations (ng/L, $\log_{10}$ scale) on each study site. Burr and Colonsay are cropland-dominated. St. Denis is grassland-dominated. Humboldt is characterized by roughly equal proportions of herbaceous vegetation and cropland near nest boxes. Different letters indicate statistically significant pairwise comparisons ($p < 0.05$) of model-estimated means, between sites, for each compound. Clothianidin (CLO) values less than the method detection limit (MDL) have been replaced by the MDL (7.4 ng/L).

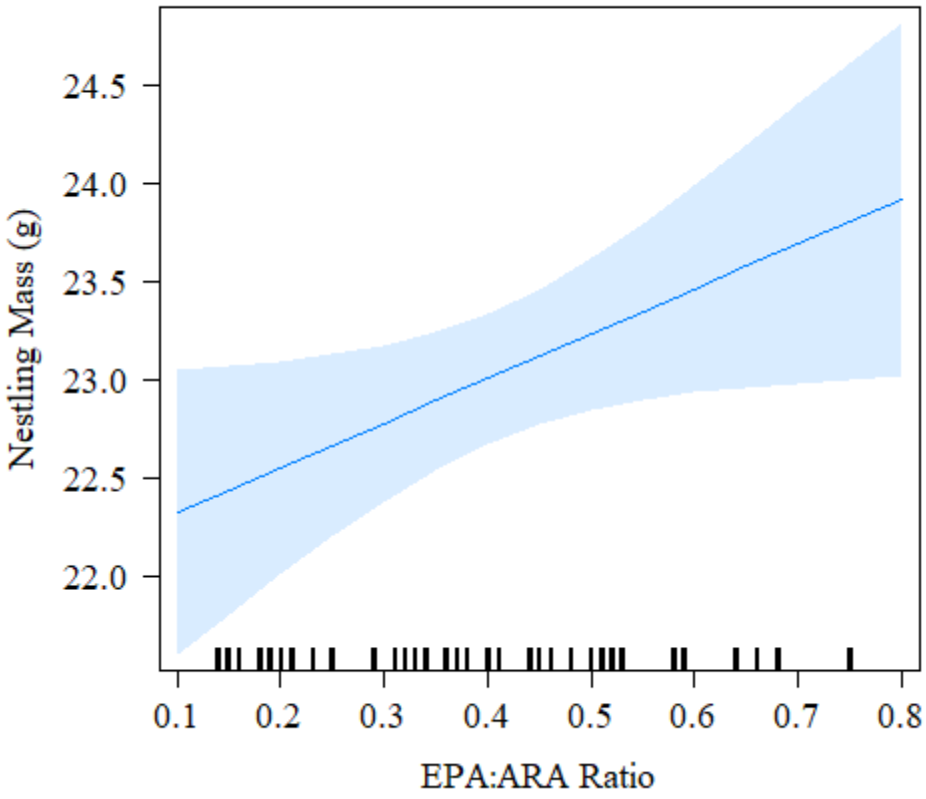

Figure 3.6. Effect plot for EPA:ARA ratio from model of nestling mass as measured on day 12 post-hatching. Shaded area represents a 95% confidence interval. Rug plot along the x-axis indicates realized values for EPA:ARA ratio.

CHAPTER 4: SYNTHESIS AND RECOMMENDATIONS FOR FUTURE RESEARCH

4.1 SYNTHESIS

My overall aim in this thesis was to assess the use of prairie ponds as foraging areas by breeding Tree Swallows in agricultural landscapes of the PPR and to investigate the diet quality of nestling swallows in relation to aquatic subsidies of omega-3 LC-PUFA and exposure to neonicotinoid insecticides. I utilized GPS-tagging and an RSF approach to assess adult breeding female Tree Swallows' habitat and space use (Chapter 2). I found that swallows reduced their use of all habitats at greater distances from the nest, but this reduction in use was less steep for prairie ponds, suggesting that swallows increased their selectivity for ponds with greater travelling distance. Interestingly, swallows appeared to strongly select for ponds even relative to vegetated areas, while sweep-net sampled insect abundance was similar or even greater in vegetation. I speculated that this discrepancy might be attributable to differences between sweep-net sampling and foraging behavior of swallows. Swallows may have increased prey capture rates over open water, relative to vegetation, and swallows might adjust their use of ponds based on spatiotemporal patterns in insect emergence and flight. Findings regarding swallow habitat selection suggest that ponds provide important foraging areas for swallows. However, breeding swallows behave as central-place foragers, such that there are limits to compensatory foraging effort. Central-place foraging swallows will likely travel farther only when the benefit(s) of doing so are equal to or outweigh the energetic cost of travelling farther from the central place (the nest). Hence, adult and their developing nestlings could benefit from productive aquatic habitat, such as ponds, in the vicinity of nests, regardless of agricultural land use.

I assessed omega-3 LC-PUFA status and neonicotinoid exposures as two components of Tree Swallow nestling diet quality possibly affected by the presence and quality of ponds in prairie agroecosystems (Chapter 3). Utilizing insect samples from the swallow study sites, I found that some aquatic insects sourced from prairie ponds could serve as an omega-3 LC-PUFA subsidy for insectivores, as reflected by higher EPA:ARA ratios in aquatic insects relative to some terrestrial taxa. Nestling Tree Swallows also differed in omega-3 LC-PUFA status (EPA:ARA ratio) across sites, possibly reflecting sweep-net sampled aquatic insect biomass or the relative availability of aquatic and terrestrial insects on each site. EPA:ARA ratios in erythrocytes displayed a positive association with nestling mass, consistent with the importance of these fatty acids to nestling Tree Swallow growth (Twining et al. 2016b). However, I found

swallows were also ubiquitously exposed to neonicotinoid insecticides. Interestingly, nestling plasma imidacloprid concentrations did not consistently differ between a grassland-dominated site and sites characterized by cropping in the immediate vicinity of nests, while concentrations of clothianidin were strongly associated with local cropping. These differences may reflect pesticide use histories, differential persistence, or different dietary sources. Neonicotinoids appear to be rapidly metabolized by birds (Bean et al. 2019), which suggests these patterns may be due to repeated local exposure. These results have important implications for the conservation of swallows and prairie ponds; however, the findings and limitations of this work also raise important research questions and provide evidence in support of more specific recommendations.

4.2 IMPLICATIONS FOR CONSERVATION OF BIODIVERSITY IN PRAIRIE AGROECOSYSTEMS

Agricultural modification of landscapes often poses threats to biodiversity, whether mediated directly (e.g., the removal of native vegetation) or indirectly (e.g., destruction of suitable habitat or reduction in prey for animals) (Tilman et al. 2002, Foley et al. 2005). Nevertheless, agricultural food production likely must increase, to some degree, to meet food demands for a growing human population (Tilman et al. 2011, Hunter et al. 2017). This suggests a need for some balance between increasing agricultural production and the conservation of biodiversity – perhaps especially so in landscapes already heavily modified by agriculture, such as the PPR, where an estimated 70% of native prairie and associated wetland basins have been converted to agricultural land use (Kissinger and Rees 2009, NABCI Canada 2012).

One means of mitigating some impacts of agricultural land use on biodiversity is the preservation of native and/or natural habitats in landscapes otherwise heavily modified by agricultural practices. Results here suggest prairie ponds, among other aquatic habitats, can serve as such critical habitat in prairie agroecosystems, providing important foraging areas and a source of nutrient rich insect prey to swallows. The importance of prairie ponds is not restricted to swallows; indeed, nutrient subsidies from ponds are probable for a variety of animals, including other avian taxa such as migratory shorebirds and waterfowl which rely on ponds as foraging areas during migratory stopover and breeding. Results based on insect sampling may also suggest the importance of conserving a diversity of natural habitat types (i.e., both aquatic and terrestrial), as both aquatic and terrestrial non-cropped habitats tended to have high

abundance of insects, though the relation of insect abundance to swallow foraging was unclear. The combination of intensive agricultural practices and expansion of agricultural land use may simultaneously depress avian biodiversity (e.g., Quinn et al. 2017), but the conservation and restoration of natural habitats in agroecosystems can mitigate some of these impacts.

Retaining prairie ponds may be critical for conservation of swallows in the PPR; however, it is likely also critical that natural habitats are conserved and restored to an intact, "natural" state to ensure benefits to biodiversity in agroecosystems. Both cropping and grazing practices have can contribute to deterioration of pond water quality (e.g., nutrient loads) and vegetative pond margins that can consequently impact insects and other invertebrates (Campbell et al. 2009), which in turn provide an important prey resource for birds. Here I found that Tree Swallows were ubiquitously exposed to neonicotinoids, presumably via dietary intake. Though it is not clear that these exposures resulted in negative impacts on swallows, this finding raises some concern about the ubiquity and environmental persistence of these pesticides and may represent a consequence of their widespread prophylactic use (e.g., Main et al. 2014). Though I have not demonstrated the dietary source of neonicotinoids, this also suggests the importance of preventing agrochemical contamination of ponds, given swallows' predisposition to exposure to contaminants in aquatic ecosystems. Maintaining intact ponds might also serve to enhance ecosystem services, such as provided by pollinators, in agroecosystems (and see Stewart et al. 2016) – though in the author's view, the conservation of biodiversity should not hinge on demonstrated benefits to humans. Changes to policy and incentives are perhaps the only certain means to ensure the retention and sustainable management of natural habitats, such as ponds, in prairie agroecosystems.

4.3 LIMITATIONS AND FUTURE RESEARCH DIRECTIONS

4.3.1 Consequences of Habitat Loss and Nutrient Limitation for Tree Swallows and Other Aerial Insectivores

I found that Tree Swallow omega-3 LC-PUFA status was not associated with agricultural land use (cropping or grazing) but may be determined by the availability of aquatic insects. Likewise, results suggested that omega-3 LC-PUFA status might be positively associated with nestling mass, while nestlings on one cropland site had higher omega-3 LC-PUFA status than those on a grassland site. Such results, in tandem with differential importance of aquatic insects

in swallow diets (Twining et al. 2018), raise the question of whether agricultural land use practice (cropping and grazing) has differential impact on Tree Swallow condition beyond reduction or disturbance of aquatic habitats and/or aquatic insect prey. Does intensive cropping and/or grazing directly affect Tree Swallow performance by altering abundance of insect prey, or are the effects reported in prior studies (e.g., Ghilain and Bélisle 2008) simply consequent to loss of aquatic insects? Importantly, agricultural intensification is not restricted to cropping practices alone, nor is even responsible grazing of livestock without environmental costs. How does Tree Swallow performance in agricultural landscapes differ from areas with less agricultural modification? I suggest future studies should consider how Tree Swallow performance is affected by land use and habitat based on simultaneous assessments of aquatic insect prey and land use practices in a factorial design (e.g., in croplands, grazed pasture, and areas with less agricultural disturbance).

Similar studies on aerial insectivores other than Tree Swallows will also be informative. Not all aerial insectivores, even among swallows, behave in precisely the same way. For example, smaller and lower-flying Barn Swallows might benefit more from the presence of non-crop vegetation than other swallows, as they may have greater ability to fly through and over such habitats to take advantage of prey inaccessible to larger swallows (Evans et al. 2003, 2007, Dreelin et al. 2018). Still, all "hawking" aerial insectivores, including Barn Swallows, exploit aquatic insects emerging from ponds and other aquatic habitat (Elgin, pers. obs.); "sallying" aerial insectivores may similarly benefit from energy and nutrient subsidies via aquatic insect prey, though foraging strategy differs (and see Twining et al. 2019). GPS-tracking of larger aerial insectivores can assist not only in characterizing migratory strategies and non-breeding locations (Fraser et al. 2017, Ng et al. 2018), but also fully characterizing local space use in breeding areas, understanding of which is likely incomplete when using visual tracking or radio-telemetry. Further miniaturization of GPS tags and development of automated telemetry systems (Lenske and Nocera 2018) will increase researchers' ability to fully characterize avian habitat and space use. Use of these and similar technologies on other aerial insectivorous species will help to better characterize the relative importance of different foraging habitats to species in this guild.

Results of this work suggest some relationship between fatty acid status and nestling mass; however, I am unable to exclude the possibility that swallows with greater EPA:ARA ratios are also consuming a greater quantity of insect prey. Therefore, I also suggest that future studies might attempt to parse out the contribution of dietary quantity and quality (nutrient composition) for Tree Swallows and other aerial insectivores in a field setting. Experimental studies have suggested that the micro- and macro-nutrient composition (e.g., fatty acids, calcium, vitamin E) of prey are important factors in the growth of nestling swallows (Dawson and Bidwell 2005, De Ayala et al. 2006, Twining et al. 2016b). Disentangling the impacts of diet quality and quantity in a field setting is increasingly possible with the introduction of smaller tracking and transmitter technologies. For example, radio-frequency identification tags (RFID) might be utilized to assess the delivery of prey (quantity) (Bonter and Bridge 2011, Bridge and Bonter 2011, Stanton et al. 2016). Diet composition and parameters of nutritional quality can be examined via bolus sampling and/or use of appropriate blood fractions (erythrocytes or plasma, depending on nutrients and temporal scale of interest). In a field setting, does diet composition for swallows and other aerial insectivores exhibit additive effects to (or even stronger effects than) prey quantity on nestling growth and condition? Whether performance of aerial insectivores other than Tree Swallows is highly dependent on dietary nutritional quality (such as omega-3 LC-PUFA) is also currently an open question.

4.3.2 Semi-permanent Prairie Ponds as a Source of Lipids and LC-PUFA

Prairie ponds provide foraging habitat not only for aerial insectivores, but a diversity of avian species that also benefit from aquatic nutrient subsidies not assessed here. Beyond waterfowl, perhaps the most apparent are resident and migratory shorebirds, which rely on ephemeral prairie ponds as foraging habitat during breeding or as critical refueling sites during migration (Skagen et al. 2008). As a guild, declines among North American migratory shorebird populations also appear to be among the steepest continent-wide (e.g., NABCI Canada 2019). Lipids provide a critical fuel source for migratory birds, and LC-PUFA may provide an important source of fuel and/or alter performance in migratory shorebirds (Guglielmo et al. 2002, Maillet and Weber 2006, 2007); still, differential impact of particular fatty acids (e.g., saturates, unsaturates, omega-6 LC-PUFA, and omega-3 LC-PUFA) on migratory performance remains unclear, to my knowledge (and see Guglielmo 2010). In contrast to coastal sites, I am aware of only one study assessing fatty acid intake by shorebirds migrating through the central flyway

(Rivers and Rintoul 2011); this study was not conducted in the PPR nor were clear assessments of LC-PUFA reported. Notwithstanding the need for additional experimental studies of lipid impacts on migratory performance, future work might consider the importance of ephemeral prairie ponds as a source of lipids and LC-PUFA to migratory shorebirds, among other taxa.

4.3.3 Biological Realism in Assessment of Prey Availability to Aerial Insectivores

An important limitation of this work is that I was not able to directly relate sampled insect abundance or biomass to Tree Swallow habitat selection, which I have suggested is likely a consequence of differences between sampling method and swallow foraging. Sweep-net sampling, as an active sampling method, may allow for better characterization of spatial variation in insect abundance or biomass at a single point in time. However, it is likely that sweep-net sampling is also sensitive to temporal variation in insect abundance affected by factors other than habitat types. For example, greater wind speeds can force smaller, poor-flying insects into aggregations in vegetation which might not otherwise be present. Sweep-net sampling can also overrepresent insect availability because not all insects clustered in dense vegetation will be accessible to aerial insectivorous birds. Still, in most studies, sampling the availability of insects to aerial insectivores has been based on passive insect sampling (Hussell and Quinney 1987, McCarty and Winkler 1999a, Imlay et al. 2017, McClenaghan et al. 2019a), which may be entirely unrepresentative of different insect densities across the landscape and spatiotemporal patterns therein. Aerial insectivorous birds will likely take advantage of more easily captured insect prey or dense concentrations of insects, regardless of landscape-scale insect abundance or biomass; however, only a subset of insects may truly be available to aerial insectivores.

I suggest three broad priorities for future research assessing prey availability to aerial insectivores, especially relevant to swallows: 1) characterize spatiotemporal patterns in abundance of insect prey (recognizing that aerial insectivores will exploit concentrations of insects, but only if accessible), 2) utilize multiple passive and active sampling methods when possible (e.g., sweep-net sampling, aerial passive sampling, and especially emergence traps, where applicable) and 3) characterize the composition of sampled insect assemblages, as not all insect prey are necessarily equal in nutritional value or energy content. I acknowledge there may be multiple factors contributing to differential habitat selection among aerial insectivores which are unrelated to insect abundance per se, and I recognize limitations and logistical constraints on

researchers' ability to sample prey availability. Still, future studies must attempt to incorporate additional "biological realism" when assessing the importance of insect prey to aerial insectivores.

4.3.4 Hazards of Agricultural Pesticides to Non-target Insects and Aerial Insectivores

Results discussed in Chapter 3 suggest that insectivorous Tree Swallows are exposed to neonicotinoid insecticides; exposure to insecticides among almost exclusively insectivorous birds raises further questions about the possible impacts of direct (i.e., toxic) and indirect effects (i.e., prey reduction) of agrochemicals on aerial insectivores. For example, changes in timing of insect emergence or failure to emerge (Cavallaro et al. 2017, 2018) could reduce the availability of aquatic insects to swallows; however, failed emergence or immobilization of insects might also enhance swallows' uptake of neonicotinoid insecticides. Cavallaro et al. (2017) reported that neonicotinoid exposure affected emergence success of a chironomid, *Chironomus dilutus* which was possibly attributable to entanglement in pupal exuvia during emergence itself. Similar molt-related mortality has been reported in larvae of the mosquito *Aedes aegypti* exposed to imidaloprid (Song et al. 1997). Tree Swallows are known to capture not only insects in flight, but also actively emerging, dying, or dead insects on or beneath pond surfaces or from the ground (e.g., Cohen and Dymerski 1986, Hobson and Sealy 1987, Elgin, pers. obs.). I suggest two a posteriori hypotheses for swallows' exposure to neonicotinoids in particular: 1) insects insensitive to neonicotinoid exposure contribute neonicotinoids to swallow diets and/or 2) insects' exposure to sublethal concentrations of neonicotinoid insecticides increases the probability of predation by swallows due to effects on emergence, immobilization, or disrupted avoidance behavior (e.g., Zhang and Nieh 2015, Parkinson and Gray 2019), thereby increasing swallows' consumption of these and other agrochemicals (Walker 2003). Assessing exposure of additional insectivorous species (aerial insectivores or others) might also be informative, and alternative hypotheses should be considered, including sources other than insects.

Characterizing the impact of "contaminant subsidies" in a field setting is complex. For example, environmental contamination can reduce predators' exposure to certain contaminants by eliminating prey that might otherwise be contaminated at lower concentrations. Animals which have higher contaminant loads can also be in better condition (i.e., have greater energy stores) than those with lower exposure to contaminants if greater prey intake also results in

greater contaminant exposure. Notwithstanding gaps in understanding insectivorous birds' exposure to contemporary agricultural pesticides, these difficulties suggest a future need for experimental work, or carefully planned field studies. Most clearly lacking are measures of agricultural pesticides present in insects, or other swallow dietary items, as well as factors impacting current use pesticide concentrations in prey items. To what doses of contaminants are swallows being exposed? If sourced from aquatic insects, can pond margin vegetation reduce contaminant loads in insects by limiting exposure (Main et al. 2015, 2017), or does vegetation simply serve as a reservoir for systemic pesticides? Are the concentrations of agrochemical contaminants in insect prey likely to exert sublethal impacts on insectivorous birds? The answers to these and similar questions serve an important role in assessing risks of pesticide exposures for insectivorous birds foraging in agricultural landscapes.

4.3.5 Diet Quality and Quantity as Drivers of Aerial Insectivore Population Trends

The evidence that aerial insectivore reproductive output or survival is dependent on total insect prey abundance is equivocal (Quinney et al. 1986, McCarty and Winkler 1999a, Imlay et al. 2017, McClenaghan et al. 2019a, Spiller and Dettmers 2019); however, to my knowledge, no studies have directly assessed the importance of total insect abundance to aerial insectivores other than swallows. Relatively few studies have attempted to parse out the relative contribution of different insect taxa and presumed nutritional quality to the reproductive output and/or survival of aerial insectivores, compared to assessments of total insect abundance or biomass.

There is also increasing evidence that the diet composition of some aerial insectivores has changed, with some changes being attributed to anthropogenic impacts on insect assemblages. Nocera et al. (2012) reported that the diet composition of Chimney Swifts (*Chaetura pelagica*), as inferred from guano samples in Kingston, Ontario, Canada, shifted from predominantly Coleopteran (beetle) prey to Hemipteran (true bug) prey, and this shift tracked the quantity of DDT and metabolites in guano samples. Given the relative toxicity of DDT to beetles (sensitive) and true bugs (insensitive), Nocera et al. (2012) argued that this dietary shift might be directly attributed to an altered insect assemblage consequent to DDT applications, with nutritional consequences for swifts. Pomfret et al. (2015) similarly examined the "guano-inferred" diet of Vaux's Swifts (*Chaetura vauxi*) from guano samples deposited ~1985-2011 on Vancouver Island, British Columbia. As seen with Chimney Swifts, Pomfret et al. (2015) reported greater

consumption of true bugs and lower consumption of beetles over time. This shift was reflected by an increase in δ15N signatures, which were correlated with population declines. By investigating museum specimens, English et al. (2018) reported that the isotopically inferred diet of Eastern Whip-poor-wills (*Antrostomus vociferous*) suggests a shift from higher to lower trophic level prey over the past 100 years. Whether such a trend reflects overall changes in insect abundance is unclear; I speculate based on the former studies that any impact might not be fully attributable to overall insect consumption given dietary flexibility, but changes in insect assemblages and composition of the diet.

Several studies more directly suggest that dietary nutritional quality – or indirectly, diet composition – contributes to reproductive output in some aerial insectivores and may have similar effects on survival. De Ayala et al. (2006) reported that supplementation of Barn Swallow diets with Vitamin E (an antioxidant), at intermediate doses, slightly enhanced nestling growth during the exponential growth period. Dawson and Bidwell (2005) found that supplementation of nestling Tree Swallow diets with calcium enhanced the growth rate for mass and 9th primary feathers. Indeed, acidification of aquatic ecosystems might negatively affect swallows reliant on aquatic insect prey; Blancher and McNicol (1988) reported that pond basicity (water pH of "wetlands") was positively related to several measures of Tree Swallow reproductive output, as well as nestling size and growth. Blancher and McNicol (1991) also found that aquatic mayflies (Ephemeroptera) and molluscs, both of which were provisioned to nestling swallows, were strongly reduced in acidified ponds; however, the overall biomass and emergence of Diptera tended to be greater. Nestling swallows were correspondingly fed fewer mayflies and more aquatic Diptera near acidified ponds, though overall intake of aquatic taxa was lower (Blancher and McNicol 1991). Aquatic insects may serve as a source of multiple nutrients for Tree Swallows and other hirundines, and indeed, aquatic insect prey may enhance nestling growth and fledging success more than total insect abundance and overall diet quantity (Twining et al. 2016b, 2018).

I acknowledge that Tree Swallows are represented most in studies of aerial insectivore diet quality, including results presented here, and I consider it likely that what constitutes nutritionally high-quality insect prey differs to some degree among species and geographic regions. Nevertheless, prior work suggests some changes in insect assemblages, with possible

impacts on aerial insectivore diet quality, have occurred and may represent an important driver of vital rates for some species in this guild. I observed some marked differences in swallow LC-PUFA status between study sites, which may be driven by the availability of aquatic insects. However, I also found widespread exposure to neonicotinoid insecticides among swallows nesting in prairie agroecosystems. My results suggest the importance of preserving and protecting natural habitats, such as prairie ponds in agroecosystems, to provide foraging areas and nutritionally high-quality prey for swallows. Aerial insectivore population trends are likely multifactorial (e.g., Spiller and Dettmers 2019); future work is needed to assess whether composition of insect assemblages can inform understanding of aerial insectivore population trends and whether declines in some aerial insectivore populations might be mitigated by habitat conservation.

LITERATURE CITED

Addy-Orduna, L. M., J. C. Brodeur, and R. Mateo. 2019. Oral acute toxicity of imidacloprid, thiamethoxam and clothianidin in eared doves: A contribution for the risk assessment of neonicotinoids in birds. Science of the Total Environment 650:1216–1223.

Almenar, D., J. Aihartza, U. Goiti, E. Salsamendi, and I. Garin. 2013. Hierarchical patch choice by an insectivorous bat through prey availability components. Behavioral Ecology and Sociobiology 67:311–320.

Anderson, D. J., and B. Voncdracek. 1999. Insects as indicators of land use in three ecoregions in the prairie pothole region. Wetlands 19:648–664.

Andow, D. A. 1991. Vegetational Diversity and Arthropod Population Response. Annual Review of Entomology 36:561–586.

Arab, L. 2003. Biomarkers of Fat and Fatty Acid Intake. Journal of Nutrition 133:925S–932S.

Attwood, S. J., M. Maron, A. P. N. House, and C. Zammit. 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Global Ecology and Biogeography 17:585–599.

De Ayala, R. M., R. Martinelli, and N. Saino. 2006. Vitamin E supplementation enhances growth and condition of nestling barn swallows (*Hirundo rustica*). Behavioral Ecology and Sociobiology 60:619–630.

Bartzen, B. A., K. W. Dufour, R. G. Clark, and F. D. Caswell. 2010. Trends in agricultural impact and recovery of wetlands in prairie Canada. Ecological Applications 20:525–538.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Batt, B., M. Anderson, C. Anderson, and F. Caswell. 1989. Use of prairie potholes by North American ducks. Pages 204–227 *in* A. van der Valk, editor. Northern Prairie Wetlands. Iowa State University Press, Ames, Iowa.

Bean, T. G., M. S. Gross, N. K. Karouna-Renier, P. F. P. Henry, S. L. Schultz, M. L. Hladik, K. M. Kuivila, and B. A. Rattner. 2019. Toxicokinetics of Imidacloprid-Coated Wheat Seeds in

Japanese Quail (Coturnix japonica) and an Evaluation of Hazard. Environmental Science and Technology 53:3888–3897.

Bellavance, V., M. Bélisle, J. Savage, F. Pelletier, and D. Garant. 2018. Influence of agricultural intensification on prey availability and nestling diet in Tree Swallows (*Tachycineta bicolor*). Canadian Journal of Zoology 96:1053–1065.

Benton, T. G., D. M. Bryant, L. Cole, and H. Q. P. Crick. 2002. Linking agricultural practice to insect and bird populations: A historical study over three decades. Journal of Applied Ecology 39:673–687.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends in Ecology and Evolution 18:182–188.

Bishop, C. A., A. J. Moran, M. C. Toshack, E. Elle, F. Maisonneuve, and J. E. Elliott. 2018. Hummingbirds and bumble bees exposed to neonicotinoid and organophosphate insecticides in the Fraser Valley, British Columbia, Canada. Environmental Toxicology and Chemistry 37:2143–2152.

Blancher, P. J., and D. K. McNicol. 1988. Breeding biology of tree swallows in relation to wetland acidity. Canadian Journal of Zoology 66:842–849.

Blancher, P. J., and D. K. McNicol. 1991. Tree swallow diet in relation to wetland acidity. Canadian Journal of Zoology 69:2629–2637.

Boatman, N. D., N. W. Brickle, J. D. Hart, T. P. Milsom, A. J. Morris, A. W. A. Murray, K. A. Murray, and P. A. Robertson. 2004. Evidence for the indirect effects of pesticides on farmland birds. Ibis 146:131–143.

Bodey, T. W., I. R. Cleasby, F. Bell, N. Parr, A. Schultz, S. C. Votier, and S. Bearhop. 2017. A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. Methods in Ecology and Evolution 9:946–955.

Bonmatin, J. M., C. Giorio, V. Girolami, D. Goulson, D. P. Kreutzweiser, C. Krupke, M. Liess, E. Long, M. Marzaro, E. A. Mitchell, D. A. Noome, N. Simon-Delso, and A. Tapparo. 2015. Environmental fate and exposure; neonicotinoids and fipronil. Environmental Science

and Pollution Research 22:35–67.

Bonter, D. N., and E. S. Bridge. 2011. Applications of radio frequency identification (RFID) in ornithological research: a review. Journal of Field Ornithology 82:1–10.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Brasso, R. L., and D. A. Cristol. 2008. Effects of mercury exposure on the reproductive success of tree swallows (*Tachycineta bicolor*). Ecotoxicology 17:133–141.

Brenna, J. T., M. Plourde, K. D. Stark, P. J. Jones, and Y. H. Lin. 2018. Best practices for the design, laboratory analysis, and reporting of trials involving fatty acids. American Journal of Clinical Nutrition 108:211–227.

Brett, M. T., and D. C. Müller-Navarra. 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. Freshwater Biology 38:483–499.

Brickle, N. W., D. G. C. Harper, N. J. Aebischer, and S. H. Cockayne. 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. Journal of Applied Ecology 37:742–755.

Bridge, E. S., and D. N. Bonter. 2011. A low-cost radio frequency identification device for ornithological research. Journal of Field Ornithology 82:52–59.

Britschgi, A., R. Spaar, and R. Arlettaz. 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. Biological Conservation 130:193–205.

Bryant, D. M., and A. K. Turner. 1982. Central place foraging by swallows (Hirundinidae): The question of load size. Animal Behaviour 30:845–856.

Byholm, P., S. Mäkeläinen, A. Santangeli, and D. Goulson. 2018. First evidence of neonicotinoid residues in a long-distance migratory raptor, the European honey buzzard (*Pernis apivorus*). Science of the Total Environment 639:929–933.

Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space

and habitat use by animals. Ecological Modelling 197:516–519.

Camp, A. A., and D. B. Buchwalter. 2016. Can't take the heat: Temperature-enhanced toxicity in the mayfly *Isonychia bicolor* exposed to the neonicotinoid insecticide imidacloprid. Aquatic Toxicology 178:49–57.

Campbell, B. D., R. J. Haro, and W. B. Richardson. 2009. Effects of agricultural land use on chironomid communities: Comparisons among natural wetlands and farm ponds. Wetlands 29:1070–1080.

Cavallaro, M. C. 2018. Assessing the effects of chronic neonicotinoid insecticide exposure on aquatic insects using multiple experimental approaches. Univeristy of Saskatchewan.

Cavallaro, M. C., K. Liber, J. V. Headley, K. M. Peru, and C. A. Morrissey. 2018. Community-level and phenological responses of emerging aquatic insects exposed to 3 neonicotinoid insecticides: An in situ wetland limnocorral approach. Environmental Toxicology and Chemistry 37:2401–2412.

Cavallaro, M. C., A. R. Main, K. Liber, I. D. Phillips, J. V. Headley, K. M. Peru, and C. A. Morrissey. 2019. Neonicotinoids and other agricultural stressors collectively modify aquatic insect communities. Chemosphere 226:945–955.

Cavallaro, M. C., C. A. Morrissey, J. V. Headley, K. M. Peru, and K. Liber. 2017. Comparative chronic toxicity of imidacloprid, clothianidin, and thiamethoxam to *Chironomus dilutus* and estimation of toxic equivalency factors. Environmental Toxicology and Chemistry 36:372–382.

Charnov, E. L. 1976. Optimal foraging theory: the marginal value theorem. Theoretical Population Biology 9:129–136.

Cohen, R. R., and M. L. Dymerski. 1986. Swallows taking insects from pond surfaces. The Wilson Bulletin 98:483–484.

Dahl, T. E. 2014. Status and trends of prairie wetlands in the United States 1997 to 2009. Washington, D.C.

Dahl, T. E., and M. D. Watmough. 2007. Current approaches to wetland status and trends

monitoring in prairie Canada and the continental United States of America. Canadian Journal of Remote Sensing 33:S17–S27.

Davies, S. R., C. D. Sayer, H. Greaves, G. M. Siriwardena, and J. C. Axmacher. 2016. A new role for pond management in farmland bird conservation. Agriculture, Ecosystems and Environment 233:179–191.

Dawson, R. D., and M. T. Bidwell. 2005. Dietary calcium limits size and growth of nestling tree swallows *Tachycineta bicolor* in a non-acidified landscape. Journal of Avian Biology 36:127–134.

Donald, D. B., N. P. Gurprasad, L. Quinnett-Abbott, and K. Cash. 2001. Diffuse geographic distribution of herbicides in northern prairie wetlands. Environmental Toxicology and Chemistry 20:273–279.

Donald, D. B., F. G. Hunter, E. Sverko, B. D. Hill, and J. Syrgiannis. 2005. Mobilization of pesticides on an agricultural landscape flooded by a torrential storm. Environmental Toxicology and Chemistry 24:2–10.

Donald, D. B., J. Syrgiannis, F. Hunter, and G. Weiss. 1999. Agricultural pesticides threaten the ecological integrity of northern prairie wetlands. Science of the Total Environment 231:173–181.

Dreelin, R. A., J. R. Shipley, and D. W. Winkler. 2018. Flight Behavior of Individual Aerial Insectivores Revealed by Novel Altitudinal Dataloggers. Frontiers in Ecology and Evolution 6:1–7.

Duelli, P., M. K. Obrist, and D. R. Schmatz. 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. Agriculture, Ecosystems and Environment 74:33–64.

Echols, K. R., D. E. Tillitt, J. W. Nichols, A. L. Secord, and J. P. McCarty. 2004. Accumulation of PCB congeners in nestling tree swallows (*Tachycineta bicolor*) on the Hudson River, New York. Environmental Science and Technology 38:6240–6246.

Eng, M. L., B. J. M. Stutchbury, and C. A. Morrissey. 2017. Imidacloprid and chlorpyrifos insecticides impair migratory ability in a seed-eating songbird. Scientific Reports 7:1–9.

Eng, M. L., B. J. M. Stutchbury, and C. A. Morrissey. 2019. A neonicotinoid insecticide reduces fueling and delays migration in songbirds. Science 365:1177–1180.

English, P. A., D. J. Green, and J. J. Nocera. 2018. Stable Isotopes from Museum Specimens May Provide Evidence of Long-Term Change in the Trophic Ecology of a Migratory Aerial Insectivore. Frontiers in Ecology and Evolution 6:1–13.

Environment and Climate Change Canada. 2017. North American Breeding Bird Survey - Canadian Trends Website, Data-version 2015. Environment and Climate Change Canada.

Ertl, H. M., M. A. Mora, D. E. Boellstorff, D. Brightsmith, and K. Carson. 2018. Potential effects of neonicotinoid insecticides on northern bobwhites. Wildlife Society Bulletin 42:649–655.

Evans, K. L., R. B. Bradbury, and J. D. Wilson. 2003. Selection of hedgerows by Swallows *Hirundo rustica* foraging on farmland: The influence of local habitat and weather. Bird Study 50:8–14.

Evans, K. L., J. D. Wilson, and R. B. Bradbury. 2007. Effects of crop type and aerial invertebrate abundance on foraging barn swallows *Hirundo rustica*. Agriculture, Ecosystems and Environment 122:267–273.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science 309:570–574.

Fontaneto, D., M. Tommaseo-Ponzetta, C. Galli, P. Risé, R. H. Glew, and M. G. Paoletti. 2011. Differences in fatty acid composition between aquatic and terrestrial insects used as food in human nutrition. Ecology of Food and Nutrition 50:351–367.

Fox, J. 2003. Effect Displays in R for Generalised Linear Models. Journal of Statistical Software 8:1–27.

Fox, J., and S. Weisberg. 2018. Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals. Journal of Statistical Software 87:1–27.

Fox, J., and S. Weisberg. 2019. An {R} Companion to Applied Regression. 3rd Editio. Sage, Thousand Oaks, CA.

Fraser, K. C., A. Shave, A. Savage, A. Ritchie, K. Bell, J. Siegrist, J. D. Ray, K. Applegate, and M. Pearman. 2017. Determining fine-scale migratory connectivity and habitat selection for a migratory songbird by using new GPS technology. Journal of Avian Biology 48:339–345.

Frenzel, M., J. Everaars, and O. Schweiger. 2016. Bird communities in agricultural landscapes: What are the current drivers of temporal trends? Ecological Indicators 65:113–121.

Friesen-Pankratz, B. 2004. Descriptive and experimental studies on the biotic and abiotic determinants of selected pesticide concentrations in prairie wetland water columns. University of Manitoba.

Fritz, K. A., L. J. Kirschman, S. D. Mccay, J. T. Trushenski, R. W. Warne, and M. R. Whiles. 2017. Subsidies of essential nutrients from aquatic environments correlate with immune function in terrestrial consumers. Freshwater Science 36:893–900.

Gabor, T. S., H. R. Murkin, M. P. Stainton, J. A. Boughen, and R. D. Titman. 1994. Nutrient additions to wetlands in the Interlake region of Manitoba, Canada: effects of a single pulse addition in spring. Hydrobiologia 279–280:497–510.

Garcés, R., and M. Mancha. 1993. One-step lipid extraction and fatty acid methyl esters preparation from fresh plant tissues. Analytical Biochemistry 211:139–143.

Ghilain, A., and M. Bélisle. 2008. Breeding success of tree swallows along a gradient of agricultural intensification. Ecological Applications 18:1140–1154.

Ghioni, C., J. G. Bell, and J. R. Sargent. 1996. Polyunsaturated fatty acids in neutral lipids and phospholipids of some freshwater insects. Comparative Biochemistry and Physiology 114:161–170.

Gibbons, D., C. Morrissey, and P. Mineau. 2015. A review of the direct and indirect effects of neonicotinoids and fipronil on vertebrate wildlife. Environmental Science and Pollution Research 22:103–118.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J.

Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gladyshev, M. I., M. T. Arts, and N. N. Sushchik. 2009. Preliminary Estimates of the Export of Omega-3 Highly Unsaturated Fatty Acids (EPA + DHA) from Aquatic to Terrestrial Ecosystems. Pages 179–210 *in* M. T. Arts, M. T. Brett, and M. J. Kainz, editors. Lipids in Aquatic Ecosystems. Springer Science+Business Media, LLC, New York.

Gladyshev, M. I., N. N. Sushchik, and O. N. Makhutova. 2013. Production of EPA and DHA in aquatic ecosystems and their transfer to the land. Prostaglandins and Other Lipid Mediators 107:117–126.

Gleason, J. E., and R. C. Rooney. 2017. Aquatic macroinvertebrates are poor indicators of agricultural activity in northern prairie pothole wetlands. Ecological Indicators 81:333–339.

Gleason, J. E., and R. C. Rooney. 2018. Pond permanence is a key determinant of aquatic macroinvertebrate community structure in wetlands. Freshwater Biology 63:264–277.

Goldsborough, L. G., and W. G. Crumpton. 2016. Distribution and environmental fate of pesticides in prairie wetlands. Great Plains Research 8:73–95.

Goldstein, M. I., T. E. Lacher, B. Woodbridge, M. J. Bechard, S. B. Canavelli, M. E. Zaccagnini, G. P. Cobb, E. J. Scollon, R. Tribolet, and M. J. Hooper. 1999. Monocrotophos-induced mass mortality of Swainson's hawks in Argentina, 1995-96. Ecotoxicology 8:201–214.

Government of Canada. 1991. The federal policy on wetland conservation. Pages 1–13. Canada.

Graves, E. E., K. A. Jelks, J. E. Foley, M. S. Filigenzi, R. H. Poppenga, H. B. Ernest, R. Melnicoe, and L. A. Tell. 2019. Analysis of insecticide exposure in California hummingbirds using liquid chromatography-mass spectrometry. Environmental Science and Pollution Research:15458–15466.

Grüebler, M. U., M. Morand, and B. Naef-Daenzer. 2008. A predictive model of the density of airborne insects in agricultural environments. Agriculture, Ecosystems and Environment 123:75–80.

Guglielmo, C. G. 2010. Move that fatty acid: Fuel selection and transport in migratory birds and

bats. Integrative and Comparative Biology 50:336–345.

Guglielmo, C. G., T. D. Williams, G. Zwingelstein, G. Brichon, and J. M. Weber. 2002. Plasma and muscle phospholipids are involved in the metabolic response to long-distance migration in a shorebird. Journal of Comparative Physiology B 172:409–417.

Haghighi, F., H. Galfalvy, S. Chen, Y. Huang, T. B. Cooper, A. K. Burke, M. A. Oquendo, J. J. Mann, and M. E. Sublette. 2015. DNA Methylation Perturbations in Genes Involved in Polyunsaturated Fatty Acid Biosynthesis Associated with Depression and Suicide Risk. Frontiers in Neurology 6.

Hallmann, C. A., R. P. B. Foppen, C. A. M. van Turnhout, H. de Kroon, and E. Jongejans. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature 511:341–343.

Hanson, B. J., K. W. Cummins, A. S. Cargill, and R. R. Lowry. 1985. Lipid content, fatty acid composition, and the effect of diet on fats of aquatic insects. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry 80:257–276.

Hao, C., M. L. Eng, F. Sun, and C. A. Morrissey. 2018. Part-per-trillion LC-MS/MS determination of neonicotinoids in small volumes of songbird plasma. Science of the Total Environment 644:1080–1087.

Haroune, L., R. Cassoulet, M.-P. Lafontaine, M. Bélisle, D. Garant, F. Pelletier, H. Cabana, and J.-P. Bellenger. 2015. Liquid chromatography-tandem mass spectrometry determination for multiclass pesticides from insect samples by microwave-assisted solvent extraction followed by a salt-out effect and micro-dispersion purification. Analytica Chimica Acta 891:160–170.

Hart, J. D., T. P. Milsom, G. Fisher, V. Wilkins, S. J. Moreby, A. W. A. Murray, and P. A. Robertson. 2006. The relationship between yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. Journal of Applied Ecology 43:81–91.

Heath, S. K., C. U. Soykan, K. L. Velas, R. Kelsey, and S. M. Kross. 2017. A bustle in the hedgerow: Woody field margins boost on farm avian diversity and abundance in an

intensive agricultural landscape. Biological Conservation 212:153–161.

Heinze, C. R., M. G. Hawkins, L. A. Gillies, X. Wu, R. L. Walzem, J. B. German, and K. C. Klasing. 2012. Effect of dietary omega-3 fatty acids on red blood cell lipid composition and plasma metabolites in the cockatiel, *Nymphicus hollandicus*. Journal of Animal Science 90:3068–3079.

Heldbjerg, H., A. D. Fox, P. V. Thellesen, L. Dalby, and P. Sunde. 2017. Common Starlings (*Sturnus vulgaris*) increasingly select for grazed areas with increasing distance-to-nest. PLoS ONE 12:1–18.

Hijmans, R. J. 2017. raster: Geographic Data Analysis and Modeling. R package version 2.6-7.

Hixson, S. M., B. Sharma, M. J. Kainz, A. Wacker, and M. T. Arts. 2015. Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: a fundamental dichotomy between freshwater and terrestrial ecosystems. Environmental Reviews 23:414–424.

Hixson, S. M., K. Shukla, L. G. Campbell, R. H. Hallett, M. Smith, L. Packer, and M. T. Arts. 2016. Long-Chain Omega-3 Polyunsaturated Fatty Acids Have Developmental Effects on the Crop Pest , the Cabbage White Butterfly *Pieris rapae*. PLoS ONE 11:1–14.

Hobson, K. A., and S. G. Sealy. 1987. Foraging, Scavenging, and Other Behavior of Swallows on the Ground. The Wilson Bulletin 99:111–116.

Houston, M. I., and C. S. Houston. 1998. Tree Swallow productivity near Saskatoon, Saskatchewan. North American Bird Bander 23:42–44.

Humann-Guilleminot, S., S. Clément, J. Desprat, Ł. J. Binkowski, G. Glauser, and F. Helfenstein. 2019. A large-scale survey of house sparrows feathers reveals ubiquitous presence of neonicotinoids in farmlands. Science of the Total Environment 660:1091–1097.

Hunter, M. C., R. G. Smith, M. E. Schipanski, L. W. Atwood, and D. A. Mortensen. 2017. Agriculture in 2050: Recalibrating targets for sustainable intensification. BioScience 67:386–391.

Hussell, D., and T. Quinney. 1987. Food abundance and clutch size of Tree Swallows

Tachycineta bicolor. Ibis:243–258.

Imlay, T. L., H. A. R. Mann, and M. L. Leonard. 2017. No effect of insect abundance on nestling survival or mass for three aerial insectivores. Avian Conservation and Ecology 12:4–13.

Jardine, T. D., R. Woods, J. Marshall, J. Fawcett, J. Lobegeiger, D. Valdez, and M. J. Kainz. 2015. Reconciling the role of organic matter pathways in aquatic food webs by measuring multiple tracers in individuals. Ecology 96:3257–3269.

Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology 61:65–71.

Johnson, M. E., and M. P. Lombardo. 2000. Nestling Tree Swallow (*Tachycineta bicolor*) Diets in an Upland Old Field in Western Michigan. American Midland Naturalist 144:216–219.

Jones, A., P. Harrington, and G. Turnbull. 2014. Neonicotinoid concentrations in arable soils after seed treatment applications in preceding years. Pest Management Science 70:1780–1784.

Jones, J. 2003. Tree Swallows (*Tachycineta Bicolor*): a New Model Organism? The Auk 120:591–599.

Josefsson, J., Å. Berg, M. Hiron, T. Pärt, and S. Eggers. 2013. Grass buffer strips benefit invertebrate and breeding skylark numbers in a heterogeneous agricultural landscape. Agriculture, Ecosystems and Environment 181:101–107.

van der Kamp, G., M. Hayashi, A. Bedard-Haughn, and D. Pennock. 2016. Prairie Pothole Wetlands – Suggestions for Practical and Objective Definitions and Terminology. Wetlands 36:229–235.

Kissinger, M., and W. E. Rees. 2009. Footprints on the prairies: Degradation and sustainability of Canadian agricultural land in a globalizing world. Ecological Economics 68:2309–2315.

Knapp, M., and M. Řezáč. 2015. Even the smallest non-crop habitat islands could be beneficial: Distribution of carabid beetles and spiders in agricultural landscape. PLoS ONE 10:1–21.

Krell, B., N. Röder, M. Link, R. Gergs, M. H. Entling, and R. B. Schäfer. 2015. Aquatic prey subsidies to riparian spiders in a stream with different land use types. Limnologica 51:1–7.

Kusack, J. W. 2018. Landscape-level effects of agricultural intensification on the condition and diet of nestling Barn Swallows (*Hirundo rustica*). The University of Western Ontario.

Lee, L. 2017. NADA: Nondetects and Data Analysis for Environmental Data. R package version 1.6-1.

Lenske, A. K., and J. J. Nocera. 2018. Field test of an automated radio-telemetry system: tracking local space use of aerial insectivores. Journal of Field Ornithology 89:173–187.

Lenth, R. 2018. emmeans: Estimated Marginal Means, aka Least-squares Means. R package version 1.3.1.

Lopez-Antia, A., M. E. Ortiz-Santaliestra, F. Mougeot, and R. Mateo. 2013. Experimental exposure of red-legged partridges (*Alectoris rufa*) to seeds coated with imidacloprid, thiram and difenoconazole. Ecotoxicology 22:125–138.

St. Louis, V. L., and J. C. Barlow. 1993. The reproductive success of tree swallows nesting near experimentally acidified lakes in northwestern Ontario. Canadian Journal of Zoology 71:1090–1097.

St. Louis, V. L., L. Breebaart, and J. C. Barlow. 1990. Foraging behaviour of Tree Swallows over acidified and nonacidic lakes. Canadian Journal of Zoology 68:2385–2392.

MacDonald, A. M., C. M. Jardine, P. J. Thomas, and N. M. Nemeth. 2018. Neonicotinoid detection in wild turkeys (*Meleagris gallopavo silvestris*) in Ontario, Canada. Environmental Science and Pollution Research 25:16254–16260.

Maillet, D., and J.-M. Weber. 2006. Performance-enhancing role of dietary fatty acids in a long-distance migrant shorebird: the semipalmated sandpiper. Journal of Experimental Biology 209:2686–2695.

Maillet, D., and J.-M. Weber. 2007. Relationship between n-3 PUFA content and energy metabolism in the flight muscles of a migrating shorebird: evidence for natural doping. Journal of Experimental Biology 210:413–420.

Main, A. R., J. Fehr, K. Liber, J. V. Headley, K. M. Peru, and C. A. Morrissey. 2017. Reduction of neonicotinoid insecticide residues in Prairie wetlands by common wetland plants.

Science of the Total Environment 579:1193–1202.

Main, A. R., J. V Headley, K. M. Peru, N. L. Michel, A. J. Cessna, and C. A. Morrissey. 2014. Widespread Use and Frequent Detection of Neonicotinoid Insecticides in Wetlands of Canada's Prairie Pothole Region. PLoS ONE 9.

Main, A. R., N. L. Michel, M. C. Cavallaro, J. V. Headley, K. M. Peru, and C. A. Morrissey. 2016. Snowmelt transport of neonicotinoid insecticides to Canadian Prairie wetlands. Agriculture, Ecosystems and Environment 215:76–84.

Main, A. R., N. L. Michel, J. V. Headley, K. M. Peru, and C. A. Morrissey. 2015. Ecological and Landscape Drivers of Neonicotinoid Insecticide Detections and Concentrations in Canada's Prairie Wetlands. Environmental Science and Technology 49:8367–8376.

Makhutova, O. N., N. N. Sushchik, M. I. Gladyshev, A. V. Ageev, E. G. Pryanichnikova, and G. S. Kalachova. 2011. Is the fatty acid composition of freshwater zoobenthic invertebrates controlled by phylogenetic or trophic factors? Lipids 46:709–721.

Maloney, E. M., K. Liber, J. V. Headley, K. M. Peru, and C. A. Morrissey. 2018. Neonicotinoid insecticide mixtures: Evaluation of laboratory-based toxicity predictions under semi-controlled field conditions. Environmental Pollution 243:1727–1739.

Manly, B. F. J., L. L. Mcdonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Second Edi. Kluwer Academic Publishers, Boston, Massachusetts.

Martin-Creuzburg, D., C. Kowarik, and D. Straile. 2017. Cross-ecosystem fluxes: Export of polyunsaturated fatty acids from aquatic to terrestrial ecosystems via emerging insects. Science of the Total Environment 577:174–182.

Maul, J. D., J. B. Belden, B. A. Schwab, M. R. Whiles, B. Spears, J. L. Farris, and M. J. Lydy. 2006. Bioaccumulation and trophic transfer of polychlorinated biphenyls by aquatic and terrestrial insects to tree swallows (*Tachycineta bicolor*). Environmental Toxicology and Chemistry 25:1017–1025.

McCarty, J. P. 1997. Aquatic Community Characteristics Influence the Foraging Patterns of Tree Swallows. The Condor 99:210–213.

McCarty, J. P. 2001. Use of Tree Swallows in Studies of Environmental Stress. Reviews in Toxicology 4:61–104.

McCarty, J. P. 2002. The number of visits to the nest by parents is an accurate measure of food delivered to nestlings in Tree Swallows. Journal of Field Ornithology 73:9–14.

McCarty, J. P., and D. W. Winkler. 1999a. Relative importance of environmental variables in determining the growth of nestling Tree Swallows *Tachycineta bicolor*. Ibis 141:286–296.

McCarty, J. P., and D. W. Winkler. 1999b. Foraging Ecology and Diet Selectivity of Tree Swallows Feeding Nestlings. The Condor 101:246–254.

McClenaghan, B., K. C. R. Kerr, and E. Nol. 2019a. Does prey availability affect the reproductive performance of Barn Swallows, *Hirundo rustica*, breeding in Ontario, Canada? Canadian Journal of Zoology.

McClenaghan, B., E. Nol, and K. C. R. Kerr. 2019b. DNA metabarcoding reveals the broad and flexible diet of a declining aerial insectivore. Auk 136:1–11.

Mengelkoch, J. M., G. J. Niemi, and R. R. Regal. 2004. Diet of the nestling tree swallow. The Condor 106:423–429.

Metherel, A. H., and K. D. Stark. 2016. The stability of blood fatty acids during storage and potential mechanisms of degradation: A review. Prostaglandins Leukotrienes and Essential Fatty Acids 104:33–43.

Michel, N. L., A. C. Smith, R. G. Clark, C. A. Morrissey, and K. A. Hobson. 2016. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography 39:774–786.

Michelson, C. I. 2015. Effects of agricultural land use on Tree Swallow (*Tachycineta bicolor*) reproduction, body condition and diet. University of Saskatchewan.

Michelson, C. I., R. G. Clark, and C. A. Morrissey. 2018. Agricultural land cover does not affect the diet of Tree Swallows in wetland-dominated habitats. The Condor 120:751–764.

Mineau, P., and A. Mclaughlin. 1996. Conservation of Biodiversity within Canadian Agricultural Landscapes: Integrating Habitat for Wildlife. Journal of Agricultural and Environmental

Ethics 9:93–113.

Mineau, P., and M. Whiteside. 2013. Pesticide Acute Toxicity Is a Better Correlate of U.S. Grassland Bird Declines than Agricultural Intensification. PLoS ONE 8.

Morrissey, C. A., P. Mineau, J. H. Devries, F. Sanchez-bayo, M. Liess, M. C. Cavallaro, and K. Liber. 2015. Neonicotinoid contamination of global surface waters and associated risk to aquatic invertebrates: A review. Environment International 74:291–303.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America 98:166–170.

Nebel, S., A. Mills, J. D. Mccracken, and P. D. Taylor. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation & Ecology 5:1.

Ng, J. W., E. C. Knight, A. L. Scarpignato, A. L. Harrison, E. M. Bayne, and P. P. Marra. 2018. First full annual cycle tracking of a declining aerial insectivorous bird, the common nighthawk (*Chordeiles minor*), identifies migration routes, nonbreeding habitat, and breeding site fidelity. Canadian Journal of Zoology 96:869–875.

Nocera, J. J., J. M. Blais, D. V Beresford, L. K. Finity, C. Grooms, L. E. Kimpe, K. Kyser, N. Michelutti, M. W. Reudink, and J. P. Smol. 2012. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous chimney swifts. Proceedings of the Royal Society B: Biological Sciences 279:3114–3120.

North American Bird Conservation Initiative Canada. 2012. The State of Canada's Birds, 2012. Ottawa, Canada.

North American Bird Conservation Initiative Canada. 2019. The State of Canada's Birds, 2019. Ottawa, Canada.

Orians, G. H., and N. E. Pearson. 1979. On the Theory of Central Place Foraging. Pages 155–177 *in* D. J. Horn, G. R. Stairs, and R. D. Mitchell, editors. Analysis of Ecological Systems. Ohio State University Press, Columbus, Ohio.

Ottens, H. J., M. W. Kuiper, H. Flinks, J. van Ruijven, H. Siepel, B. J. Koks, F. Berendse, and G.

R. de Snoo. 2014. Do Field Margins Enrich the Diet of the Eurasian Skylark *Alauda arvensis* on Intensive Farmland? Ardea 102:161–174.

Papp, Z., G. R. Bortolotti, M. Sebastian, and J. E. G. Smits. 2007. PCB Congener Profiles in Nestling Tree Swallows and Their Insect Prey. Environmental Contamination and Toxicology 52:257–263.

Paquette, S. R., D. Garant, F. Pelletier, and M. Bélisle. 2013. Seasonal patterns in Tree Swallow prey (Diptera) abundance are affected by agricultural intensification. Ecological Applications 23:122–133.

Paquette, S. R., F. Pelletier, D. Garant, and M. Belisle. 2014. Severe recent decrease of adult body mass in a declining insectivorous bird population. Proceedings of the Royal Society B: Biological Sciences 281:1–9.

Parkinson, R. H., and J. R. Gray. 2019. Neural conduction, visual motion detection, and insect flight behaviour are disrupted by low doses of imidacloprid and its metabolites. NeuroToxicology 72:107–113.

Patenaude-Monette, M., M. Bélisle, and J. F. Giroux. 2014. Balancing energy budget in a central-place forager: Which habitat to select in a heterogeneous environment? PLoS ONE 9:1–12.

Pebesma, E. J., and R. S. Bivand. 2005. Classes and methods for spatial data in R. R News 5.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2019. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-139.

Pisa, L. W., V. Amaral-Rogers, L. P. Belzunces, J. M. Bonmatin, C. A. Downs, D. Goulson, D. P. Kreutzweiser, C. Krupke, M. Liess, M. Mcfield, C. A. Morrissey, D. A. Noome, J. Settele, N. Simon-Delso, J. D. Stark, J. P. Van Der Sluijs, H. Van Dyck, and M. Wiemers. 2014. Effects of neonicotinoids and fipronil on non-target invertebrates. Environmental Science and Pollution Research 22:68–102.

PMRA. 2004. Clothianidin - Regulatory note (REG2004-06).

Polis, G. A., W. B. Anderson, and R. D. Holt. 2002. Toward an Integration of Landscape and

Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs. Annual Review of Ecology and Systematics 28:289–316.

Pomfret, J. K., J. J. Nocera, T. K. Kyser, and M. W. Reudink. 2015. Linking Population Declines with Diet Quality in Vaux's Swifts. Northwest Science 88:305–313.

Popova, O. N., A. Y. Haritonov, N. N. Sushchik, O. N. Makhutova, G. S. Kalachova, A. A. Kolmakova, and M. I. Gladyshev. 2017. Export of aquatic productivity, including highly unsaturated fatty acids, to terrestrial ecosystems via Odonata. Science of the Total Environment 581–582:40–48.

Poulin, B., G. Lefebvre, and L. Paz. 2010. Red flag for green spray: Adverse trophic effects of *Bti* on breeding birds. Journal of Applied Ecology 47:884–889.

QGIS Development Team. 2018. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

Quinn, J. E., T. Awada, F. Trindade, L. Fulginiti, and R. Perrin. 2017. Combining habitat loss and agricultural intensification improves our understanding of drivers of change in avian abundance in a North American cropland anthrome. Ecology and Evolution 7:803–814.

Quinn, J. E., J. R. Brandle, and R. J. Johnson. 2012. The effects of land sparing and wildlife-friendly practices on grassland bird abundance within organic farmlands. Agriculture, Ecosystems and Environment 161:10–16.

Quinney, T. E., and C. D. Ankney. 1985. Prey Size Selection by Tree Swallows. The Auk 102:245–250.

Quinney, T. E., D. J. T. Hussell, and C. D. Ankney. 1986. Sources of Variation in Growth of Tree Swallows. The Auk 103:389–400.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rainho, A., A. M. Augusto, and J. M. Palmeirim. 2010. Influence of vegetation clutter on the capacity of ground foraging bats to capture prey. Journal of Applied Ecology 47:850–858.

Rappole, J. H., and A. R. Tipton. 1991. New Harness Design for Attachment of Radio

Transmitters to Small Passerines. Journal of Field Ornithology 62:335–337.

Rivers, J. W., and D. A. Rintoul. 2011. Fatty acid composition of depot fat of shorebirds collected at mid-continental stopover sites during spring migration. Journal of Field Ornithology 82:225–231.

Rodewald, P. (Editor). 2015. The Birds of North America.

Rudy, M. D., M. J. Kainz, M. Graeve, S. M. Colombo, and M. T. Arts. 2016. Handling and storage procedures have variable effects on fatty acid content in fishes with different lipid quantities. PLoS ONE 11.

Sánchez-Bayo, F., K. Goka, and D. Hayasaka. 2016. Contamination of the Aquatic Environment with Neonicotinoids and its Implication for Ecosystems. Frontiers in Environmental Science 4:1–14.

Sargent, J. R., J. G. Bell, M. V. Bell, R. J. Henderson, and D. R. Tocher. 1995. Requirement criteria for essential fatty acids. Journal of Applied Ichthyology 11:183–198.

Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, J. Pardieck, K L, J. E. Fallon, and W. A. Link. 2017. The North American Breeding Bird Survey, Results and Analysis 1966 - 2015. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD.

Schindler, D. E., and A. P. Smits. 2017. Subsidies of Aquatic Resources in Terrestrial Ecosystems. Ecosystems 20:78–93.

Schoener, T. W. 1979. Generality of the Size-Distance Relation in Models of Optimal Feeding. The American Naturalist 114:902–914.

Shutler, D., R. G. Clark, C. Fehr, and A. W. Diamond. 2006. Time and Recruitment Costs as Currencies in Manipulation Studies on the Costs of Reproduction. Ecology 87:2938–2946.

Shutler, D., A. Mullie, and R. G. Clark. 2000. Bird Communities of Prairie Upland and Wetlands in Relation to Farming Practices in Saskatchewan. Conservation Biology 14:1441–1451.

Simopoulos, A. P. 1991. Omega-3 fatty acids in health and disease and in growth and development. American Journal of Clinical Nutrition 54:438–463.

Skagen, S. K., D. A. Granfors, and C. P. Melcher. 2008. On Determining the Significance of

Ephemeral Continental Wetlands To North American Migratory Shorebirds. The Auk 125:20–29.

Smith, A. C., M.-A. R. Hudson, C. M. Downes, and C. M. Francis. 2015. Change points in the population trends of aerial-insectivorous birds in North America: Synchronized in time across species and regions. PLoS ONE 10:1–23.

Smits, J. E. G., G. R. Bortolotti, M. Sebastian, and J. J. H. Ciborowski. 2005. Spatial, temporal, and dietary determinants of organic contaminants in nestling Tree Swallows in Point Pelee National Park, Ontario, Canada. Environmental Toxicology and Chemistry 24:3159–3165.

Song, M. Y., J. D. Stark, and J. J. Brown. 1997. Comparative toxicity of four insecticides, including imidacloprid and tebufenozide, to four aquatic arthropods. Environmental Toxicology and Chemistry 16:2494–2500.

Spiller, K. J., and R. Dettmers. 2019. Evidence for multiple drivers of aerial insectivore declines in North America. The Condor 121:1–13.

Stanley-Samuelson, D. W., R. A. Jurenka, C. Cripps, G. J. Blomquist, and M. de Renobales. 1988. Fatty acids in insects: Composition, metabolism, and biological significance. Archives of Insect Biochemistry and Physiology 9:1–33.

Stanton, R. L. 2015. Indirect effects of agricultural intensification on tree swallow (*Tachycineta bicolor*) foraging behaviour, body condition, and physiology. University of Saskatchewan.

Stanton, R. L., C. A. Morrissey, and R. G. Clark. 2016. Tree Swallow (*Tachycineta bicolor*) foraging responses to agricultural land use and abundance of insect prey. Canadian Journal of Zoology 94:637–642.

Stanton, R. L., C. A. Morrissey, and R. G. Clark. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agriculture, Ecosystems & Environment 254:244–254.

Statistics Canada. 2016. Table 004-0203 - Census of Agriculture, land use, every 5 years, CANSIM.

Statistics Canada. 2018. National Road Network.

http://ftp.maps.canada.ca/pub/nrcan_rncan/vector/geobase_nrn_rrn/sk/.

Stewart, R. E., and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. Page Resource Publication 92. Bureau of Sport Fisheries and Wildlife, Fish and Wildlife Service, United States Department of the Interior, Washington, D.C.

Stewart, R. I. A., G. K. S. Andersson, C. Brönmark, B. K. Klatt, L.-A. Hansson, V. Zülsdorff, and H. G. Smith. 2016. Ecosystem services across the aquatic–terrestrial boundary: Linking ponds to pollination. Basic and Applied Ecology 18.

Streby, H. M., T. L. McAllister, S. M. Peterson, G. R. Kramer, J. A. Lehman, and D. E. Andersen. 2015. Minimizing marker mass and handling time when attaching radio-transmitters and geolocators to small songbirds. The Condor 117:249–255.

Sullivan, S. M. P., and A. D. Rodewald. 2012. In a state of flux: The energetic pathways that move contaminants from aquatic to terrestrial environments. Environmental Toxicology and Chemistry 31:1175–1183.

Taliansky-Chamudis, A., P. Gómez-Ramírez, M. León-Ortega, and A. J. García-Fernández. 2017. Validation of a QuECheRS method for analysis of neonicotinoids in small volumes of blood and assessment of exposure in Eurasian eagle owl (*Bubo bubo*) nestlings. Science of the Total Environment 595:93–100.

Tangen, B. A., M. G. Butler, and M. J. Ell. 2003. Weak correspondence between macroinvertebrate assemblages and land use in Prairie Pothole Region wetlands, USA. Wetlands 23:104–115.

Therneau, T. M. 2015. A package for Survival Analysis in S. version 2.38.

Therneau, T. M., and P. M. Grambsch. 2000. Modeling Survival Data: Extending the Cox Model. Springer, New York.

Thomas, C. F. G., and E. J. P. Marshall. 1999. Arthropod abundance and diversity in differently vegetated margins of arable fields. Agriculture, Ecosystems and Environment 72:131–144.

Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable

intensification of agriculture. Proceedings of the National Academy of Sciences of the United States of America 108:20260–20264.

Tilman, D., K. G. Cassman, P. A. Matson, R. Naylor, and S. Polasky. 2002. Agricultural sustainability and intensive production practices. Nature 418:671–677.

Tiner, R. W. 2003. Geographically isolated wetlands of the United States. Wetlands 23:494–516.

Tomizawa, M., and J. E. Casida. 2005. Neonicotinoid Insecticide Toxicology: Mechanisms of Selective Action. Annual Review of Pharmacology and Toxicology 45:247–268.

Torres-Ruiz, M., J. D. Wehr, and A. A. Perrone. 2007. Trophic relations in a stream food web: importance of fatty acids for macroinvertebrate consumers. Journal of the North American Benthological Society 26:509–522.

Torres-Ruiz, M., J. D. Wehr, and A. A. Perrone. 2010. Are net-spinning caddisflies what they eat? An investigation using controlled diets and fatty acids. Journal of the North American Benthological Society 29:803–813.

Triplehorn, C. A., and N. F. Johnson. 2005. Borror and Delong's Introduction to the Study of Insects. Seventh edition. Thomson-Brooks/Cole, Belmont, California.

Twining, C. W., J. T. Brenna, N. G. Hairston, and A. S. Flecker. 2016a. Highly unsaturated fatty acids in nature: What we know and what we need to learn. Oikos 125:749–760.

Twining, C. W., J. T. Brenna, P. Lawrence, J. R. Shipley, T. N. Tollefson, and D. W. Winkler. 2016b. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. Proceedings of the National Academy of Sciences 113:10920–10925.

Twining, C. W., J. T. Brenna, P. Lawrence, D. W. Winkler, A. S. Flecker, and N. G. Hairston. 2019. Aquatic and terrestrial resources are not nutritionally reciprocal for consumers. Functional Ecology:1–11.

Twining, C. W., P. Lawrence, D. W. Winkler, A. S. Flecker, and J. T. Brenna. 2017. Conversion efficiency of alpha linolenic acid to long-chain omega-3 highly unsaturated fatty acids in aerial insectivore chicks. Journal of Experimental Biology.

Twining, C. W., J. R. Shipley, and D. W. Winkler. 2018. Aquatic insects rich in omega-3 fatty acids drive breeding success in a widespread bird. Ecology Letters.

Walker, C. 2003. Neurotoxic pesticides and behavioural effects upon birds. Ecotoxicology 12:307–316.

Watmough, M. D., and M. J. Schmoll. 2007. Environment Canada's Prairie & Northern Region Habitat Monitoring Program Phase II: Recent habitat trends in the Prairie Habitat Joint Venture. Page Technical Report Series Number 493. Environment Canada, Canadian Wildlife Service Prairie and Northern Region, Edmonton, Alberta.

Wickham, H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Winkler, D. W., K. K. Hallinger, D. R. Ardia, R. J. Robertson, B. J. Stutchbury, and R. R. Cohen. 2011. Tree Swallow (*Tachycineta bicolor*), version 2.0. In the Birds of North America (P.G. Rodewald, editor). Cornell Lab of Ornithology, Ithaca, New York, USA. Cornell Lab of Ornithology, Ithaca, New York.

Winkler, D. W., M. K. Luo, and E. Rakhimberdiev. 2013. Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). Oecologia 173:129–138.

Wrubleski, D. A., and L. C. M. Ross. 2011. Aquatic Invertebrates of Prairie Wetlands: Community Composition, Ecological Roles, and Impacts of Agriculture. Pages 91–116 *in* K. D. Floate, editor. Arthropods of Canadian Grasslands (Volume 2): Inhabitants of a Changing Landscape. Biological Survey of Canada.

Zhang, E., and J. C. Nieh. 2015. The neonicotinoid imidacloprid impairs honey bee aversive learning of simulated predation. Journal of Experimental Biology 218:3199–3205.

APPENDIX A

Table A1. Model parameters for the resource selection function. SE, standard error; SD, standard deviation; COR, correlation.

	Estimate	SE	Z	p
(Intercept)	-3.13	0.19	-16.41	<0.001
Habitat Vegetation	0.34	0.23	1.48	0.14
Habitat Water	-0.66	0.39	-1.72	0.09
Distance from Nest (km)	-7.74	0.99	-7.85	<0.001
Habitat Vegetation : Distance from Nest (km)	-0.19	0.90	-0.21	0.83
Habitat Water : Distance from Nest (km)	6.16	1.32	4.66	<0.001
SD (Intercept) Box	0.60	-	-	-
SD Habitat Cropland, Box	0.48	-	-	-
SD Habitat Vegetation, Box	0.44	-	-	-
SD Habitat Water, Box	1.27	-	-	-
COR Habitat Cropland, Habitat Vegetation; Box	-0.87	-	-	-
COR Habitat Cropland, Habitat Water; Box	-0.76	-	-	-
COR Habitat Vegetation, Habitat Water; Box	0.50	-	-	-
SD Distance from Nest (km), Box	1.37	-	-	-
SD Habitat Cropland: Distance from Nest (km), Box	3.91	-	-	-
SD Habitat Vegetation : Distance from Nest (km), Box	3.98	-	-	-
SD Habitat Water : Distance from Nest (km), Box	2.40	-	-	-
COR Habitat Cropland: Distance from Nest (km), Habitat Vegetation : Distance from Nest (km); Box	0.84	-	-	-
COR Habitat Cropland: Distance from Nest (km), Habitat Water : Distance from Nest (km); Box	-0.86	-	-	-
COR Habitat Vegetation : Distance from Nest (km), Habitat Water : Distance from Nest (km); Box	-0.46	-	-	-

Table A2. Analysis of deviance table (Type II Wald Chi-square tests) for the resource selection function. df, degrees of freedom.

	χ^2	df	p
Habitat	9.27	2	0.010
Distance from Nest (km)	77.31	1	<0.001
Habitat : Distance from Nest (km)	29.52	2	<0.001

Table A3. Contrasts of a main effects only resource selection function. Odds ratios are presented, but contrasts were conducted on the log odds ratio scale. P-values adjusted using Tukey method for comparing a family of three estimates. SE, standard error.

Contrast	Odds Ratio	SE	Z-ratio	p
Non-crop Vegetation v. Cropland	1.38	0.25	1.81	0.16
Water v. Cropland	2.44	0.42	5.12	<0.001
Water v. Vegetation	1.76	0.28	3.55	0.001

Table A4. Parameters for model of detection at the nest. SE, standard error; SD, standard deviation.

	Estimate	SE	Z	p
(Intercept)	6.38	1.60	4.00	<0.001
Mean Temperature	-0.24	0.05	-5.15	<0.001
Total Precipitation	-0.13	0.11	-1.21	0.22
Maximum Gust Speed (Low)	0.28	0.18	1.52	0.13
Nestling Age	-0.36	0.14	-2.67	0.01
Site Colonsay	0.47	0.26	1.81	0.07
Site St. Denis	0.18	0.25	0.72	0.47
Site Humboldt	-0.03	0.25	-0.11	0.91
SD (Intercept) Box	0.29	-	-	-

Table A5. Analysis of deviance table (Type II Wald Chi-square tests) for model of detection at nest. df, degrees of freedom.

	χ^2	df	p
Mean Temperature	26.50	1	<0.001
Total Precipitation	1.47	1	0.22
Maximum Gust Speed	2.32	1	0.13
Nestling Age	7.12	1	0.01
Site	5.33	3	0.15

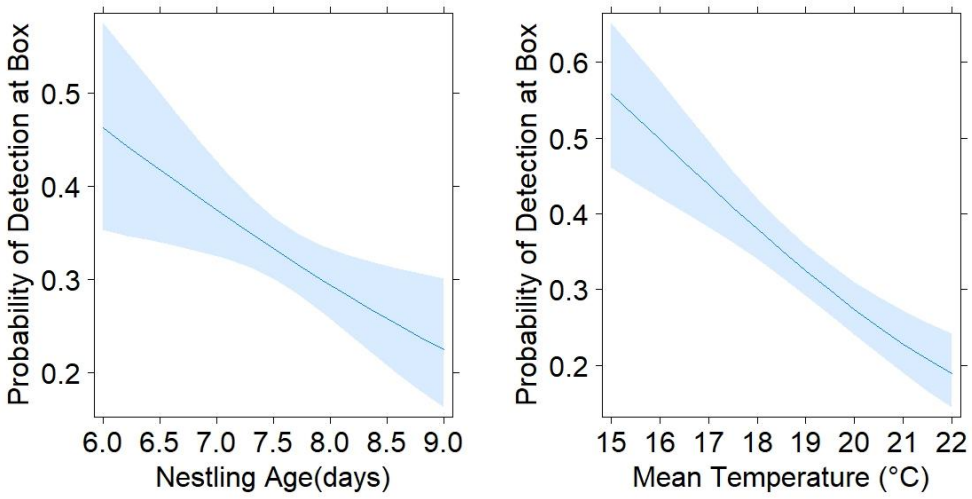

Figure A1. Effect displays for significant effects from model of detection at the nest. Left, predictions of the nestling age effect. Right, predictions of mean temperature effect.

Table A6. Parameters for model of detection distance from the nest. SE, standard error; SD, standard deviation.

	Estimate	SE	t-value	p
(Intercept)	4.83	4.26	1.13	0.26
Mean Temperature	-0.30	0.12	-2.42	0.02
Total Precipitation	0.31	0.29	1.08	0.28
Maximum Gust Speed (Low)	-0.25	0.50	-0.49	0.62
Site Colonsay	0.02	0.67	0.03	0.98
Site St. Denis	0.29	0.68	0.43	0.67
Site Humboldt	-0.97	0.67	-1.46	0.15
Nestling Age	0.68	0.37	1.84	0.07
SD (Intercept) Box	0.87	-	-	-
SD Observation Residual	1.00	-	-	-

Table A7. Analysis of deviance table (Type II Wald Chi-square tests) for model of detection distance from the nest.

	χ^2	df	p
Mean Temperature	5.88	1	0.02
Total Precipitation	1.16	1	0.28
Maximum Gust Speed	0.24	1	0.62
Site	6.00	3	0.11
Nestling Age	3.38	1	0.07

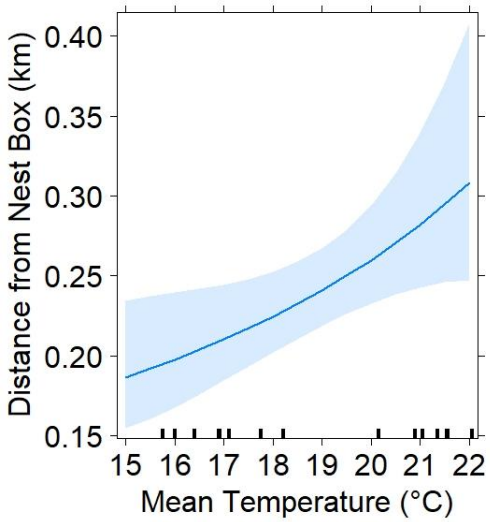

Figure A2. Effect plot for daily mean temperature effect from model of detection distance from the nest. Rug plot along the x-axis indicates realized values for daily mean temperature.

Table A8. Parameters for model of sweep-net insect abundance in 2017. SE, standard error; SD, standard deviation.

	Estimate	SE	Z	p
(Intercept)	0.72	0.34	2.12	0.03
Site Type Grassland	-0.03	0.48	-0.07	0.95
Habitat Upland	-3.75	0.48	-7.78	<0.001
Habitat Pond	-0.22	0.34	-0.64	0.52
Period Late	-0.35	0.35	-1.01	0.31
Site Type Grassland : Habitat Upland	3.46	0.65	5.33	<0.001
Site Type Grassland : Habitat Pond	-0.62	0.49	-1.27	0.20
Site Type Grassland : Period Late	-1.17	0.50	-2.33	0.02
Habitat Upland : Period Late	1.80	0.65	2.77	0.01
Habitat Pond : Period Late	0.10	0.48	0.21	0.83
Site Type Grassland : Habitat Upland : Period Late	-1.45	0.90	-1.61	0.11
Site Type Grassland : Habitat Pond : Period Late	1.67	0.70	2.40	0.02
SD (Intercept) Site	0.34	-	-	-

Table A9. Analysis of deviance table (Type II Wald Chi-square tests) for model of sweep-net insect abundance in 2017. df, degrees of freedom.

	χ^2	df	p
Site Type	0.01	1	0.94
Habitat	42.09	2	<0.001
Period	5.40	1	0.02
Site Type : Habitat	39.94	2	<0.001
Site Type : Period	5.65	1	0.02
Habitat : Period	8.49	2	0.01
Site Type : Habitat : Period	13.87	2	<0.001

Table A10. Contrasts of model-estimated marginal means for sweep-net insect abundance in 2017. Model-estimated ratios of geometric means and standard errors are provided on the response scale for abundance; tests were performed on the log scale. P-values adjusted using Tukey method for comparing a family of 12 estimates. SE, standard error.

Contrast	Ratio	SE	Z-Ratio	p
Cropland,Margin,Early / Grassland,Margin,Early	1.03	0.50	0.07	1.00
Cropland,Margin,Early / Cropland,Upland,Early	42.62	20.57	7.78	<0.001
Cropland,Margin,Early / Grassland,Upland,Early	1.38	0.75	0.60	1.00
Cropland,Margin,Early / Cropland,Pond,Early	1.25	0.43	0.64	1.00
Cropland,Margin,Early / Grassland,Pond,Early	2.39	1.15	1.81	0.81
Cropland,Margin,Early / Cropland,Margin,Late	1.42	0.49	1.01	1.00
Cropland,Margin,Early / Grassland,Margin,Late	4.71	2.31	3.16	0.07
Cropland,Margin,Early / Cropland,Upland,Late	9.98	4.28	5.37	<0.001

Cropland,Margin,Early / Grassland,Upland,Late	4.43	2.39	2.76	0.20
Cropland,Margin,Early / Cropland,Pond,Late	1.60	0.55	1.36	0.97
Cropland,Margin,Early / Grassland,Pond,Late	1.86	0.89	1.29	0.98
Grassland,Margin,Early / Cropland,Upland,Early	41.29	24.38	6.30	<0.001
Grassland,Margin,Early / Grassland,Upland,Early	1.34	0.58	0.67	1.00
Grassland,Margin,Early / Cropland,Pond,Early	1.21	0.59	0.39	1.00
Grassland,Margin,Early / Grassland,Pond,Early	2.32	0.81	2.40	0.40
Grassland,Margin,Early / Cropland,Margin,Late	1.37	0.67	0.65	1.00
Grassland,Margin,Early / Grassland,Margin,Late	4.56	1.65	4.18	<0.01
Grassland,Margin,Early / Cropland,Upland,Late	9.67	5.31	4.13	<0.001
Grassland,Margin,Early / Grassland,Upland,Late	4.29	1.82	3.44	0.03
Grassland,Margin,Early / Cropland,Pond,Late	1.55	0.75	0.90	1.00
Grassland,Margin,Early / Grassland,Pond,Late	1.80	0.63	1.68	0.88
Cropland,Upland,Early / Grassland,Upland,Early	0.03	0.02	-5.38	<0.001
Cropland,Upland,Early / Cropland,Pond,Early	0.03	0.01	-7.28	<0.001
Cropland,Upland,Early / Grassland,Pond,Early	0.06	0.03	-4.89	<0.001
Cropland,Upland,Early / Cropland,Margin,Late	0.03	0.02	-7.05	<0.001
Cropland,Upland,Early / Grassland,Margin,Late	0.11	0.07	-3.69	0.01
Cropland,Upland,Early / Cropland,Upland,Late	0.23	0.13	-2.64	0.25
Cropland,Upland,Early / Grassland,Upland,Late	0.10	0.07	-3.55	0.02
Cropland,Upland,Early / Cropland,Pond,Late	0.04	0.02	-6.81	<0.001
Cropland,Upland,Early / Grassland,Pond,Late	0.04	0.03	-5.32	<0.001
Grassland,Upland,Early / Cropland,Pond,Early	0.90	0.49	-0.19	1.00
Grassland,Upland,Early / Grassland,Pond,Early	1.73	0.73	1.31	0.98
Grassland,Upland,Early / Cropland,Margin,Late	1.03	0.56	0.05	1.00
Grassland,Upland,Early / Grassland,Margin,Late	3.41	1.46	2.86	0.16
Grassland,Upland,Early / Cropland,Upland,Late	7.23	4.32	3.31	0.04
Grassland,Upland,Early / Grassland,Upland,Late	3.21	1.56	2.40	0.41
Grassland,Upland,Early / Cropland,Pond,Late	1.16	0.62	0.27	1.00
Grassland,Upland,Early / Grassland,Pond,Late	1.35	0.56	0.71	1.00
Cropland,Pond,Early / Grassland,Pond,Early	1.92	0.93	1.36	0.97
Cropland,Pond,Early / Cropland,Margin,Late	1.14	0.40	0.37	1.00
Cropland,Pond,Early / Grassland,Margin,Late	3.78	1.86	2.71	0.22
Cropland,Pond,Early / Cropland,Upland,Late	8.01	3.41	4.88	<0.001
Cropland,Pond,Early / Grassland,Upland,Late	3.56	1.92	2.35	0.44
Cropland,Pond,Early / Cropland,Pond,Late	1.28	0.44	0.73	1.00
Cropland,Pond,Early / Grassland,Pond,Late	1.49	0.72	0.83	1.00
Grassland,Pond,Early / Cropland,Margin,Late	0.59	0.29	-1.08	1.00
Grassland,Pond,Early / Grassland,Margin,Late	1.97	0.70	1.90	0.76
Grassland,Pond,Early / Cropland,Upland,Late	4.17	2.28	2.61	0.27
Grassland,Pond,Early / Grassland,Upland,Late	1.85	0.78	1.46	0.95
Grassland,Pond,Early / Cropland,Pond,Late	0.67	0.32	-0.84	1.00
Grassland,Pond,Early / Grassland,Pond,Late	0.78	0.27	-0.74	1.00
Cropland,Margin,Late / Grassland,Margin,Late	3.32	1.63	2.44	0.38

Cropland,Margin,Late / Cropland,Upland,Late	7.04	3.04	4.52	<0.001
Cropland,Margin,Late / Grassland,Upland,Late	3.13	1.69	2.11	0.62
Cropland,Margin,Late / Cropland,Pond,Late	1.13	0.39	0.34	1.00
Cropland,Margin,Late / Grassland,Pond,Late	1.31	0.63	0.56	1.00
Grassland,Margin,Late / Cropland,Upland,Late	2.12	1.17	1.36	0.97
Grassland,Margin,Late / Grassland,Upland,Late	0.94	0.41	-0.14	1.00
Grassland,Margin,Late / Cropland,Pond,Late	0.34	0.17	-2.21	0.54
Grassland,Margin,Late / Grassland,Pond,Late	0.39	0.14	-2.62	0.27
Cropland,Upland,Late / Grassland,Upland,Late	0.44	0.27	-1.36	0.97
Cropland,Upland,Late / Cropland,Pond,Late	0.16	0.07	-4.29	<0.01
Cropland,Upland,Late / Grassland,Pond,Late	0.19	0.10	-3.08	0.09
Grassland,Upland,Late / Cropland,Pond,Late	0.36	0.19	-1.90	0.76
Grassland,Upland,Late / Grassland,Pond,Late	0.42	0.18	-2.06	0.65
Cropland,Pond,Late / Grassland,Pond,Late	1.17	0.56	0.32	1.00

Table A11. Parameters for model of sweep-net insect abundance in 2018. SE, standard error; SD, standard deviation.

	Estimate	SE	Z	p
(Intercept)	1.36	0.45	2.99	<0.01
Site Type Grassland	-0.15	0.71	-0.21	0.84
Habitat Upland	-2.45	0.51	-4.80	<0.001
Habitat Pond	-0.94	0.45	-2.09	0.04
Site Type Grassland : Habitat Upland	3.00	0.75	3.99	<0.001
Site Type Grassland : Habitat Pond	0.90	0.75	1.21	0.23
SD (Intercept) Site	0.57	-	-	-

Table A12. Analysis of deviance table (Type II Wald Chi-square tests) for model of sweep-net insect abundance in 2018. df, degrees of freedom.

	χ^2	df	p
Site Type	2.29	1	0.13
Habitat	8.40	2	0.02
Site Type : Habitat	15.97	2	<0.001

Table A13. Contrasts of model-estimated marginal means for sweep-net insect abundance in 2018. Model-estimated ratios and standard errors are provided on the response scale for abundance; tests were performed on the log scale. P-values adjusted using Tukey method for comparing a family of 6 estimates. SE, Standard Error.

Contrast	Ratio	SE	Z-ratio	p
Margin,Cropland / Upland,Cropland	11.56	5.89	4.80	<0.001
Margin,Cropland / Pond,Cropland	2.56	1.15	2.09	0.29
Margin,Cropland / Margin,Grassland	1.16	0.82	0.21	1.00

Margin,Cropland / Upland,Grassland	0.67	0.51	-0.53	0.99
Margin,Cropland / Pond,Grassland	1.20	0.87	0.25	1.00
Upland,Cropland / Pond,Cropland	0.22	0.11	-2.95	0.04
Upland,Cropland / Margin,Grassland	0.10	0.08	-3.06	0.03
Upland,Cropland / Upland,Grassland	0.06	0.05	-3.55	0.01
Upland,Cropland / Pond,Grassland	0.10	0.08	-2.93	0.04
Pond,Cropland / Margin,Grassland	0.45	0.31	-1.14	0.87
Pond,Cropland / Upland,Grassland	0.26	0.20	-1.79	0.47
Pond,Cropland / Pond,Grassland	0.47	0.34	-1.05	0.90
Margin,Grassland / Upland,Grassland	0.57	0.32	-1.00	0.92
Margin,Grassland / Pond,Grassland	1.04	0.60	0.06	1.00
Upland,Grassland / Pond,Grassland	1.80	1.20	0.89	0.95

Table A14. Parameters for model of sweep-net insect biomass in 2017. SE, standard error; SD, standard deviation.

	Estimate	SE	t-value
(Intercept)	1.92	0.36	5.40
Site Type Grassland	-1.57	0.50	-3.13
Habitat Upland	-4.40	0.52	-8.47
Habitat Pond	-1.14	0.42	-2.70
Period Late	0.25	0.42	0.60
Site Type Grassland : Habitat Upland	4.49	0.73	6.12
Site Type Grassland : Habitat Pond	1.58	0.60	2.64
Site Type Grassland : Period Late	-0.18	0.60	-0.30
Habitat Upland : Period Late	1.47	0.73	2.00
Habitat Pond : Period Late	0.41	0.60	0.69
Site Type Grassland : Habitat Upland : Period Late	-0.91	1.04	-0.88
Site Type Grassland : Habitat Pond : Period Late	0.06	0.85	0.07
SD (Intercept) Site	0.27	-	-
SD Observation Residual	0.85	-	-

Table A15. Analysis of deviance table (Type II Wald F-tests with Kenward-Roger degrees of freedom) for model of sweep-net insect biomass in 2017. df, degrees of freedom.

	F	df	df (residual)	p
Site Type	0.40	1	2	0.59
Habitat	22.45	2	66	<0.001
Period	8.26	1	66	0.01
Site Type : Habitat	30.43	2	66	<0.001
Site Type : Period	0.80	1	66	0.38
Habitat : Period	1.93	2	66	0.15
Site Type : Habitat : Period	0.50	2	66	0.61

Table A16. Parameters for simplified model of sweep-net insect biomass in 2017. SE, standard error; SD, standard deviation.

	Estimate	SE	t-value
(Intercept)	1.77	0.30	5.89
Site Type Grassland	-1.66	0.40	-4.11
Habitat Upland	-3.66	0.37	-9.93
Habitat Pond	-0.94	0.30	-3.11
Period Late	0.54	0.19	2.86
Site Type Grassland : Habitat Upland	4.03	0.52	7.74
Site Type Grassland : Habitat Pond	1.61	0.43	3.79
SD (Intercept) Site	0.27	-	-
SD Observation Residual	0.85	-	-

Table A17. Contrasts of model-estimated marginal means from simplified model of sweep-net insect biomass in 2017. Estimates and standard errors are provided on the transformed (ln(mu+1)) scale for biomass. SE, standard error; df, degrees of freedom.

Contrast	Estimate	SE	df	t-ratio	p
Upland,Cropland - Margin,Cropland	-3.66	0.37	71	-9.93	<0.001
Pond,Cropland - Margin,Cropland	-0.94	0.30	71	-3.11	0.03
Pond,Cropland - Upland,Cropland	2.73	0.37	71	7.39	<0.001
Margin,Grassland - Margin,Cropland	-1.66	0.40	4.47	-4.11	0.07
Margin,Grassland - Upland,Cropland	2.00	0.46	7.18	4.39	0.02
Margin,Grassland - Pond,Cropland	-0.72	0.40	4.47	-1.79	0.54
Upland,Grassland - Margin,Cropland	-1.29	0.46	7.18	-2.83	0.16
Upland,Grassland - Upland,Cropland	2.37	0.50	10.37	4.71	0.01
Upland,Grassland - Pond,Cropland	-0.35	0.46	7.18	-0.77	0.96
Upland,Grassland - Margin,Grassland	0.37	0.37	71	1.00	0.91
Pond,Grassland - Margin,Cropland	-0.99	0.40	4.47	-2.44	0.31
Pond,Grassland - Upland,Cropland	2.68	0.46	7.18	5.87	<0.01
Pond,Grassland - Pond,Cropland	-0.05	0.40	4.47	-0.12	1.00
Pond,Grassland - Margin,Grassland	0.68	0.30	71	2.24	0.23
Pond,Grassland - Upland,Grassland	0.30	0.37	71	0.83	0.96

Table A18. Contrasts of model-estimated marginal means for sweep-net insect biomass by sweep period in 2017. Estimates and standard error are provided on the transformed (ln(mu+1)) scale for biomass. SE, standard error; df, degrees of freedom.

Contrast	Estimate	SE	df	t-ratio	p
Early - Late	-0.54	0.19	71	-2.86	0.01

Table A19. Parameters for model of sweep-net insect biomass in 2018. SE, standard error; SD, standard deviation.

Term	Estimate	SE	t-value
(Intercept)	1.43	0.68	2.12
Site Type Grassland	-0.02	1.07	-0.02
Habitat Upland	-2.41	0.58	-4.19
Habitat Pond	-0.82	0.47	-1.74
Site Type Grassland : Habitat Upland	2.51	0.87	2.87
Site Type Grassland : Habitat Pond	0.01	0.74	0.01
SD (Intercept) Site	1.02	-	-
SD Observation Residual	1.15	-	-

Table A20. Analysis of deviance table (Type II Wald F-tests with Kenward-Roger degrees of freedom) for model of sweep-net insect biomass in 2018. df, degrees of freedom.

	F	df	df (residual)	p
Site Type	0.29	1	2.99	0.63
Habitat	5.11	2	42.01	0.01
Site Type : Habitat	5.01	2	42.02	0.01

Table A21. Contrasts of model-estimated marginal means for sweep-net insect biomass in 2018. Model-estimated ratios and standard errors are provided on the response scale; tests were performed on the transformed (log) scale. P-values adjusted using Tukey method for comparing a family of 6 estimates. SE, standard error. df, degrees of freedom.

Contrast	Ratio	SE	df	t-ratio	p
Margin,Cropland / Upland,Cropland	11.15	6.41	42.00	4.19	<0.01
Margin,Cropland / Pond,Cropland	2.26	1.06	42.00	1.74	0.52
Margin,Cropland / Margin,Grassland	1.02	1.09	4.11	0.02	1.00
Margin,Cropland / Upland,Grassland	0.93	1.03	4.85	-0.07	1.00
Margin,Cropland / Pond,Grassland	2.29	2.45	4.11	0.78	0.96
Upland,Cropland / Pond,Cropland	0.20	0.12	42.00	-2.77	0.08
Upland,Cropland / Margin,Grassland	0.09	0.10	4.92	-2.14	0.40
Upland,Cropland / Upland,Grassland	0.08	0.10	5.72	-2.14	0.38
Upland,Cropland / Pond,Grassland	0.21	0.23	4.92	-1.41	0.72
Pond,Cropland / Margin,Grassland	0.45	0.48	4.11	-0.74	0.96
Pond,Cropland / Upland,Grassland	0.41	0.46	4.85	-0.80	0.96
Pond,Cropland / Pond,Grassland	1.01	1.08	4.11	0.01	1.00
Margin,Grassland / Upland,Grassland	0.91	0.60	42.05	-0.15	1.00
Margin,Grassland / Pond,Grassland	2.24	1.29	42.00	1.40	0.73
Upland,Grassland / Pond,Grassland	2.47	1.63	42.05	1.38	0.74

APPENDIX B

Table B1. Summary of eicosapentaenoic acid: arachidonic acid (EPA:ARA) ratios by taxon and site. Allan and St. Denis are grassland-dominated sites. Burr and Colonsay are cropland-dominated sites. Humboldt has roughly equal area of herbaceous vegetation and cropland in the sampling area. Trichopteran samples were pooled across the Allan, Colonsay, and Humboldt sites. Hemiptera were pooled across all sites, with Humboldt more heavily represented by biomass. Lepidoptera were pooled across all sites, with Burr more heavily represented by biomass. CV, coefficient of variation; ND, not detected.

Taxon	Site	Replicates	EPA:ARA Ratio	CV
Trichoptera	Pooled	1	7.38	-
Zygoptera	Allan	3	6.09	1.54
Zygoptera	Burr	3	5.85	0.30
Zygoptera	Colonsay	3	7.00	1.08
Zygoptera	Humboldt	3	7.39	1.58
Zygoptera	St. Denis	3	6.01	1.01
Nematocera	Allan	3	4.00	3.96
Nematocera	Burr	2	4.43	0.05
Nematocera	Colonsay	2	2.29	5.68
Nematocera	Humboldt	3	4.72	3.10
Nematocera	St. Denis	2	3.62	3.20
Brachycera	Allan	3	2.06	1.24
Brachycera	Burr	3	2.57	3.64
Brachycera	Colonsay	3	2.86	3.22
Brachycera	Humboldt	3	3.15	2.42
Brachycera	St. Denis	3	1.89	4.66
Coleoptera	Allan	3	0.11	5.30
Coleoptera	Burr	3	1.12	1.50
Coleoptera	Colonsay	1	1.63	-
Coleoptera	Humboldt	3	1.00	4.44
Coleoptera	St. Denis	1	1.15	-
Orthoptera	Allan	3	1.96	6.78
Orthoptera	Burr	1	0.55	-
Orthoptera	Colonsay	1	0.58	-
Orthoptera	Humboldt	1	EPA, ARA ND	-
Orthoptera	St. Denis	2	EPA, ARA ND	-
Hemiptera	Pooled	3	3.79	5.01
Hymenoptera	Allan	1	3.91	-
Hymenoptera	Burr	3*	2.68	9.25
Hymenoptera	Colonsay	1	ARA ND	-
Hymenoptera	Humboldt	2*	7.23	-
Hymenoptera	St. Denis	1	EPA, ARA ND	-
Lepidoptera	Pooled	2	ARA ND	-

*ARA not detected in one sample

Table B2. Parameter estimates of linear model of log-transformed EPA:ARA ratios by study site. SE, standard error.

	Estimate	SE	t	p
(Intercept)	-1.64	0.06	-25.96	<0.001
Site Colonsay	1.04	0.09	11.63	<0.001
Site St. Denis	0.71	0.09	8.01	<0.001
Site Humboldt	0.84	0.09	9.66	<0.001

Table B3. Parameter estimates of generalized least squares model of log-transformed plasma imidacloprid concentrations by study site. SE, standard error; SD, standard deviation.

	Estimate	SE	t	p
(Intercept)	5.61	0.24	23.36	<0.001
Site Colonsay	-0.88	0.35	-2.52	0.02
Site St. Denis	-1.12	0.48	-2.31	0.03
Site Humboldt	0.56	0.28	2.01	0.05
	Standard deviation parameter estimates			
Site	Burr	Colonsay	St. Denis	Humboldt
SD	1	1.06	1.75	0.57

Table B4. Parameter estimates of parametric survival model of plasma clothianidin concentrations by study site. SE, standard error.

	Estimate	SE	z	p
(Intercept)	3.07	0.20	15.64	<0.001
Site Colonsay	0.70	0.28	2.51	0.01
Site St. Denis	-1.31	0.33	-4.02	<0.001
Site Humboldt	0.35	0.29	1.19	0.23
Log (scale)	-0.43	0.13	-3.37	0.001

Table B5. Parameter estimates of linear mixed-effects model of nestling body mass. SE, standard error; SD, standard deviation.

	Estimate	SE	t
(Intercept)	-6.64	3.37	-1.97
Head-bill	1.12	0.12	9.72
Brood Size	-0.09	0.21	-0.44
EPA:ARA Ratio	2.28	1.07	2.12
Total Neonicotinoids	0.00	0.00	-0.74
SD (Intercept) Box	0.99	-	-
SD Observation Residual	1.13	-	-

Table B6. Analysis of deviance table (Type II Wald F-tests with Kenward-Roger degrees of freedom) for linear mixed-effects model of nestling body mass. df, degrees of freedom.

	F	df	df (residual)	p
Head-bill	93.67	1	243.28	<0.001
Brood Size	0.19	1	39.49	0.66
EPA:ARA Ratio	4.51	1	38.99	0.04
Total Neonicotinoids	0.55	1	40.76	0.46